SYNAPSID BURROWS IN THE LOWER JURASSIC NAVAJO SANDSTONE, UTAH

By

David Joseph Riese

Submitted to the graduate degree program in Geology and the Graduate Faculty of the University of Kansas in partial fulfillment of the requirements for the degree of Master of Science.

_____
Co-Chairperson: Stepthen T. Hasiotis

_____
Co-Chairperson: Larry D. Martin

_____
Robert H. Goldstein

Date Defended: 04/21/11

The thesis committee for David J. Riese

certifies that this is the approved version of the following thesis:

SYANPSID BURROWS IN THE LOWER JURASSIC NAVAJO SANDSTONE, UTAH

_____

Stephen T. Hasiotis, Chairman

_____

Larry D. Martin, Co-Chairman

Date approved: 04/21/11

ABSTRACT

David J. Riese
Department of Geology, some date
University of Kansas

Enigmatic structures below interdune deposits of the Lower Jurassic Navajo Sandstone near Moab, Utah are interpreted as synapsid burrows based on similar morphologies to fossil and extant synapsid burrows. Two types of burrows are distinguished by their size. Type I burrows are large diameter and comprise complex, high density sinuous tunnels, Y- and T- branched tunnels, sinuous ramps, and chambers. Type I burrows at one locality weather into mounds averaging 33 m x 22 m and extend ~ 1 m above the surface. Type I burrows are dorsoventrally flattened, in cross section averaging 9.3 cm wide and 4.2 cm high, and are sand filled and structureless. These burrows mostly have smooth walls, though some have scalloped walls. Type I burrows represent a new ichnogenera and ichnospecies *Labyrinthopolis odieri*. These burrows are best explained by multiple individuals living together in social groups similar to modern vole (social) and mole rats (eusocial), and likely represent permanent dwelling structures for foraging, nesting, hiding, and food storage. Type II burrows are mega diameter with simple, inclined tunnels ~ 35 cm wide and ~ 20 cm high, and exhibit well-preserved bilobate morphology along the underside of the tunnel. The walls preserve a series of 3 or 4 thin (~ 4–8 mm), inclined scratch marks from the upper part of the wall and along the floor. Type II burrows represents a new ichnogenera and ichnospecies *Schemalitus psalihyponomes*. Type II burrows were likely constructed by therapsids based on similarities to therapsid burrows found in South Africa and Antarctica, and likely represents a permanent shelter used for dwelling and brooding. Alternate excavators for Type I and II burrows are rejected by reviewing and comparing burrow morphologies of fossil and extant vertebrate groups because morphologies are consistent within

the major groups in both fossil and extant vertebrates. Burrow morphologies reflect the tracemaker's anatomy, social structure, media consistency, and food availability.

ACKNOWLEDGEMENTS

The completion of this thesis could not have been done without the assistance of many people. My advisor Stephen T. Hasiotis assisted me with initial field work in Utah, and also provided his in-depth knowledge of ichnology and sedimentology, discussed potential ideas with me, as well as providing his editorial aid that greatly improved this thesis. My co-chair Larry D. Martin assisted me with his in-depth knowledge of therapsids, early mammals, and mammal burrows, editorial aid that greatly improved this thesis as well as assistance in guiding me to new ideas. My committee member Robert Goldstein assisted me with petrographic analysis, editorial aid that grealy improved this thesis. I would also like to send a special thanks to the late Georges Odier who was one of the first to document the burrows in the Navajo Sandstone. His assistance, concern, and hospitality towards me during my summer field work were greatly appreciated. I would also like to thank Alicia Rosales who provided support for not only field work, but also with reviews, and most importantly moral support through this whole process. Thanks also to D. Lobue, J. Schmerge, A. Falk, R. Moore, J. Retrum, W. Jones, B. Platt, and C. Congreve for ideas, editorial reviews, and moral support. Lastly, I would like to thank my family for moral and financial support when I was having difficult situations throughout this process. Funds were provided by: The University of Kansas Department of Geology, Geological Society of America graduate student research grant, and the American Association of Petroleum Geologists Grants-in-Aid.

TABLE OF CONTENTS

FIGURES AND TABLES

FIGURE 24—Photographs of *Labyrinthopolis odieri* n. igen. and n. isp. *1, L. odieri* with Y-branching (KUVP 150601). *2, L. odieri* with weak sinuous morphology (KUVP 150597). *3, L. odieri* with a curved morphology (KUVP 150598). *4–5,* Straight segment of *L. odieri* (KUVP 150599–150600). *6, L. odieri* with sinuous morphology (Holotype specimen KUVP 150596). Scales are all 10 cm.

FIGURE 25—Surficial morphology of *Labyrinthopolis odieri* n. igen. and n. isp. *1,* Plaster cast of a mole burrow with scallop marks produced from the claw pushing on the surface of the burrow. Scallops pointed out by white arrows. *2,* Scallop marks on *L odieri* pointed out by arrows constructed by organism pushing along the walls with their claws. Also notice most specimens of *L. odieri* have a smooth surface (KUVP 150602). *3,* Invertebrate bioturbation observed as small cylindrical projections on *L. odieri* (KUVP 150603). One black or white bar on scale = 1 cm.

FIGURE 26—Architectural morphology of *Labyrinthopolis odieri* n. igen. and n. isp. *1,* Site 1 locality that shows *L. odieri* occurring in high density mounded areas. Person for scale is ~ 5′6″. *2–3,* Close up of mounded areas showing different architectural elements of *L. odieri* displaying multiple branching. *4,*Branching morphology of *L. odieri*. *5*, Sinuous morphology of *L. odieri*. One black or white bar on scale = 1 cm

FIGURE 27—Scatter plot of width to height of *Labyrinthopolis odieri* n. igen. and n. isp. and *Schemalitus psalihyponomes* n. igen. and n. isp.

FIGURE 28—Architectural and surficial morphologies of *Schemalitus psalihyponomes* n. igen. and n. isp. *1, S. psalihyponomes* seen extending from the sandstone where it is poorly preserved, into a mudstone where it is well preserved. Person for scale is ~ 5′6″ (KUVP 150594). *2–3,* Well preserved *S. psalihyponomes* seen in mudstone with a raised floor creating a bilobate

morphology (KUVP 150594). *4,* Cross sectional view of *S. psalihyponomes* that has a massive fill (KUVP 150595). *5–6,* Scratch marks pointed out by white arrows on the upper sides and bottom of lobes on *S. psalihyponomes* (KUVP 150594).

FIGURE 29—Summary diagram of morphologies seen in *Labyrinthopolis odieri* n. igen. and n. isp. and *Schemalitus psalihyponomes* n. igen. and n. isp.

FIGURE 30—Common terms used to describe architectural and surficial morphologies of burrows. Modified from Hasiotis et al. (2007).

FIGURE 31—Architecture of lungfish burrows with lungfish inside. A). Burrow of *Protopterus annectens*. Notice cap of the entrance and cocoon. Modified from Johnels and Svensson (1954). B–C). Burrows of *Lepidosiren.* Modified from Kerr (1898).

FIGURE 32—Architecture of fish burrows. A). Top and side view of a *Lesueurigobius friesii* burrow. B). Top and side view of an *L. friesii* burrow constructed in an aquarium. C) Top view of a *L. friesii* burrow occupied by two gobies that used separate parts of the burrow. This burrow may have been originally excavated by crabs. Modified after Rice and Johnstone (1972). D). *Boleophthalmus* burrow with two entrances. Note towards the top of the burrow the smaller crab burrows viewed as black lines as well as different fill pattern then the main burrow. E). *Boleophthalmus* burrow with one entrance also with crab burrow located near the entrance. F). *Boleophthalmus* burrow with two entrances. Modified from Clayton and Vaughan (1986). G). Second burrow morphology of the yellowhead jawfish *Opistognathus aurifrons*. Note the stones within the pit creating stability, and the material surrounding the terminal chamber. Modified from Colin (1973).

FIGURE 33—Architecture of fish burrows. Burrows with other fill pattern excavated by crabs. A). Architecture of the red band fish *Cepola rubescens* burrows with a branch that does not reach

the surface and a lateral deflection towards the base. Modified from Atkinson and Pullin (1996). B). Vertical *C. rubescens* burrow with interconnecting crab burrows near the entrance. Modified from Atkinson et al. (1977). C). *Lonchopisthus micrognathus* burrow with a main opening and a secondary opening to the right. D). *L. micrognathus* burrow without any secondary opening. Modified from Colin and Arneson (1978). E). Top and side view of *Lumpenus lampretaeformis* burrow. Burrow has two openings with third side tunnel not does reach the surface. F) Top and side view of a more complex *L. lampretaeformis* burrow. Modified from Atkinson et al. (1987).

FIGURE 34—Burrow morphologies of 5 species of *Heleioporus*. Top line of burrow in each part represents the surface line. A). *H. psammophilus*; B). *H. eyrei*; C). *H. inornatus*; D). *H. barycragus*; E). *H. albopunctatus*. Modified from Bailey and Roberts (1981).

FIGURE 35—Architecture of lysorophid burrows. A–B). Type I architectural morphology. C). Type II architectural morphology. Modified from Hembree et al. (2004).

FIGURE 36—Plan view showing direction of 12 gopher tortoise burrows. Each burrow is a separate tunnel. Modified from Hallinan (1923).

FIGURE 37—Architecture of amphisbeanian burrows exant and fossil.

FIGURE 38—Architecture of monitor lizard burrows. A). *Varanus bengalensis* burrow in a vertical bank. Note loose sediment piled up in the tunnel. B). Typical longitudinal profile of a *V. bengalensis* burrow. C). Typical longitudinal profile of a *V. bengalensis* burrow with obstructions in subsurface. Modified from Auffenberg (1983). D–E). Top and side view of two *Varanus salvator* burrows. Modified from Traeholt (1995).

FIGURE 39—Burrows of iguanas. A). Typical morphology of a Dipsosaurus burrow. Modified from Norris (1953). B). Morphology of a complex multiseason *Iguana iguana* burrow from a top view. Side view is a cross section from A to B. C). Morphology of a single season simple *I.*

CHAPTER ONE. INTRODUCTION

This thesis presents evidence that enigmatic structures in the Lower Jurassic Navajo Sandstone near Moab, Utah, are burrows constructed by synapsids: mammals and therapsids. This thesis will also discuss interpretations of the behaviors represented by the burrows, and their paleoenvironmental and paleoecological significance.

The objectives of this thesis are to: (1) interpret the origin of enigmatic structures in the Lower Jurassic Navajo Sandstone; (2) demonstrate the usage of morphologic criteria to aid in identification of structures from other biogenic and abiogenic structures with similar morphologies; (3) name the structures using proper ichnotaxonomic classification rules; and (4) provide an up-to-date review of morphologic descriptions of fossil and extant vertebrate burrows.

This thesis is divided into three manuscripts (i.e., chapters). The first manuscript (Chapter 2) discusses the architectural and surficial morphology of the structures, and their use in determining their origin as burrows excavated by mammals or therapsids. This manuscript also discusses the paleoecological implications of burrows and their association with rhizoliths, invertebrate bioturbation, fluid-escape pipes, and wind-eroded features. The second manuscript (Chapter 3) describes and places the structures—identified as burrows—into two new ichnotaxa, and compares them with other fossil vertebrate burrows. The third manuscript (Chapter 4) is a review of the architectural and surficial morphologies of fossil and extant vertebrate burrows of amphibians, reptiles, therapsids, and mammals.

Fossil biota in the Navajo Sandstone are recognized based on plant, invertebrate, and vertebrate body fossils that include ostracodes, sphenophytes, tritylodontids, theropod dinosaurs, crocodylomorphs, and prosauropods (Winkler et al., 1991; Irmis, 2005; Parrish and Falcon-Lang,

2007). Trace fossils, however, have been recognized mostly as evidence for invertebrate life in these eolian deposits (e.g., Ahlbrandt et al., 1978; Ekdale and Picard, 1985; Tanner et al., 2006; Ekdale et al., 2007; Hasiotis et al., 2007a; Loope, 2008). Ichnotaxa in the Navajo Sandstone likely produced by arthropods includes *Planolites beverleyensis*, *Palaeophycus tubularis*, *Skolithos linearis*, *Arenicolites ispp*, and *Naktodemasis* [*Taenidium*] *serpentinus* (e.g., Loope and Rowe, 2003; Loope et al., 2004a; Ekdale et al., 2007). Rhizoliths, large silicified coniferous tree trunks, and stumps provide evidence for plant life in the Navajo Sandstone (Loope, 1988; Hasiotis et al., 2007a; Parrish and Falcon-Lang, 2007). Vertebrate trace fossils in the Navajo Sandstone include dinosaur and reptile tracks, and burrows (e.g., Baird, 1980; Lockley et al., 1992, 1998; Lockley and Hunt, 1995; Rainforth and Lockley, 1996; Loope and Rowe, 2003; Irmis, 2005; Lockley, 2005; 2006b; Seiler and Chan, 2008).

Trace fossils represent an interaction between an organism and the media that illustrates behavior. The vertebrate trace fossil record includes tracks, trails, burrows, nests, bite marks, coprolites, cololites, gastroliths, and regurgitites. These traces have been attributed to fish, amphibians, reptiles, dinosaurs, mammals and birds in lithologies representing fluvial floodplain, lacustrine, or palustrine environments (e.g., Smith, 1987; Groenewald et al., 2001; Miller et al., 2001; Hasiotis et al., 2004, 2007b; Gobetz and Martin, 2006). Relatively few vertebrate trace fossils, besides tracks, have been identified in eolian deposits (Martin and Bennett, 1977; Voorhies, 1975b; Albrandt et al., 1978; Loope, 2006a; Loope, 2008). Trace fossils may represent a hidden biodiversity in the fossil record (Hasiotis and Bourke, 2006; Hasiotis et al., 2007).

Vertebrate burrows in the fossil record have recently received more attention. Voorhies (1975b) and Hasiotis et al. (2007) provided brief reviews of vertebrate burrows. The earliest

record of vertebrate burrows is of lungfish in Devonian fluvial deposits of the Catskill Formation in central Pennsylvania (Hasiotis, 2002; Hasiotis et al., 2007).

Extant vertebrates burrow in nearly every continental environment on Earth, including eolian settings (Ahlbrandt et al., 1978; Kinlaw, 1999; Hasiotis et al., 2007b). Vertebrates excavate burrows for protection, mating, food gathering, aestivation, hibernation, and dwelling (Kinlaw, 1999; Hasiotis, 2002; Hasiotis et al., 2007).

Rarely, fossil vertebrate burrows have associated body fossils. Identifying a potential excavator of a burrow, therefore, can be problematic because the body fossil record has low preservation potential. Body fossils found associated with vertebrate burrows and identified as the excavator comprise amphibians (Olson and Bolles, 1975), lungfish (Romer and Olson, 1954; Carlson, 1968; Olson and Bolles, 1975; Dalquest and Carpenter, 1977; Hasiotis et al., 1993), therapsids (Smith, 1987; Groenewald et al., 2001; Damiani et al., 2003), bear dogs (Hunt et al., 1983), beavers (Martin and Bennett, 1977), and mammals (Voorhies, 1974, 1975a).

Trace fossils have a greater preservation potential then body fossils, and therefore, more commonly burrows are identified as vertebrate and the excavators determined by the burrows architectural and surficial morphologies by comparisons to extant vertebrate burrows of the same group (e.g., Smith, 1987; Groenewald et al., 2001; Miller et al., 2001; Hasiotis et al., 2004, 2007; Loope, 2006, 2008). Fossil vertebrates likely excavated burrows for the same behavioral and physiological reasons extant organisms do today which include ecological and environmental reasons, so the architectural morphologies between fossils and extant vertebrates are similar. Architectural morphologies of vertebrate burrows can vary for a variety of reasons, including the type of organism and its excavation method(s), number of individuals living the in the structure, media consistency, food availability, and reason for burrowing (e.g., Jarvis and Sale, 1971;

Davies and Jarvis, 1986; Spinks et al., 2000). Architectural morphology is defined by the burrow diameter (width and height), length of each segment, type (Y, T) and angle of branching, orientations, burrow shapes, and area dimensions of each burrow system. Architectural morphology also includes the complexity and connectivity of structures. Horizontal burrows are termed tunnels, while vertical burrows are shafts. Chambers are enlarged areas that can be found at the end of a shaft or tunnel and are called terminal chambers, or can be found within the burrow complex. Surficial morphology includes such patterns on burrow walls as scratches, ridges, or knobs that indicate excavation or locomotion methods.

Excavators, identified based on architectural and surficial morphologies, include lungfish (Carroll, 1965), amphibians (Hembree et al., 2004, 2005), reptiles (Hasiotis et al., 2004; Hembree and Hasiotis, 2006), therapsids (Miller et al., 2001; Lucas et al., 2006), rodents (e.g., Bown and Kraus, 1983; Gobetz, 2006; Gobetz and Martin, 2006), beavers (Barbour 1892, 1897), enigmatic mammals (Hasiotis, 2002; Hasiotis et al., 2004; Hembree and Hasiotis, 2008), and an enigmatic excavator (Loope, 2006a). Identification of the excavator is further complicated when organisms other than the original excavator occupy the burrow after it is abandoned (e.g., Auffenberg and Weaver 1969; Voorhies, 1975).

Although many fossil vertebrate burrows are being discovered, many of them have not been place in ichnotaxonomic scheme, but instead are place in an open nomenclature. Ichnogeneric and ichnospecies names should be based on the morphology of the burrow, because several organisms can create similarly looking traces, which can also vary based on media consistency (Magwood, 1992; Seilacher, 1992; Pickerill, 1994; Bromley, 1996).

REFERENCES

AUFFENBERG, W., and WEAVER, W.G., JR., 1969, *Gopherus berlanceri* in southeastern Texas: Florida State Museum Bulletin, v. 13, p. 141–203.

BARBOUR, E.H., 1892, Notice of new gigantic fossils: Science, v. 19, p. 99–100.

BARBOUR, E.H., 1897, Nature, structure, and phylogeny of *Daimonelix:* Bulletin of the Geological Society of America, v. 8, p. 99–100.

BOWN, T.M., and KRAUS, M.J., 1983, Ichnofossils of the alluvial Willwood Formation (Lower Eocene), Big Horn Basin, northwest Wyoming, U.S.A: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 43, p. 95–128.

CARLSON, K.J., 1968, The skull morphology and aestivation burrows of the Permian lungfish, *Gnathorhiza serrata*: Journal of Geology, v. 76, p. 62–71.

CARROLL, R.L., 1965, Lungfish burrows from the Michigan Coal Basin: Science, v. 148, p. 963–964.

DALQUEST, W.W., and CARPENTER, R.M., 1977, A new discovery of fossil lungfish burrows: Texas Journal of Science, v. 26, p. 611.

DAVIES, K.C., and JARVIS, J.U.M., 1986, The burrow systems and burrowing dynamics of the mole–rats *Bathygergus hottentotus* in the fynbos of the south–western Cape, South Africa: The Zoological Society of London, v. 209, p. 125–147.

GOBETZ, K.E., 2006, Possible burrows of mylagaulids (Rodentia: Aplodontoidea: Mylagaulidae) from the late Miocene (Barstovian) Pawnee Creek Formation, northeastern Colorado: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 237, p. 119–136.

GOBETZ, K.E., and MARTIN, L.D., 2006, Burrows of a gopher-like rodent, possibly Gregorymys (Geomyoidea: Geomyidae: Entoptychtinae), from the early Miocene Harrison Formation, Nebraska: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 237, p. 305–314.

HASIOTIS, S.T., 2002, Continental trace fossils: SEPM Short Course Notes, v. 51 p. 1–132.

HASIOTIS, S.T., 2004, Reconnaissance of Upper Jurassic Morrison Formation ichnofossils, Rocky Mountain Region, USA: paleoenvironmental, stratigraphic, and paleoclimatic significance of terrestrial and freshwater ichnocoenoses: Sedimentary Geology, v. 167, p. 177–268.

HASIOTIS, S.T., and BOURKE, M.C., 2006, Continental trace fossils and museum exhibits: displaying burrows as organism behavior frozen in time: The Geological Curator, v. 8, p. 211–226.

HASIOTIS, S.T., MITCHELL, C.E., and DUBIEL, R.F., 1993, Application of morphologic burrow interpretations to discern continental burrow architects: lungfish or crayfish?: Ichnos, v. 2, p. 315–333.

HASIOTIS, S.T., WELLNER, R.W., MARTIN, A., DEMKO, T.M., 2004, Vertebrate burrows from Triassic and Jurassic continental deposits of North America and Antarctica: their paleoenvironmental and paleoecological significance: Ichnos, v. 11, p. 103–124.

HASIOTIS, S.T., PLATT, B.F., HEMBREE, D.I., and EVERHEART, M.J., 2007, The trace-fossil record of vertebrates, *in* Miller, W. III eds., Trace Fossils—Concepts, Problems, Prospects: Elsevier Press, Amsterdam, p. 196–218.

HEMBREE, D.I., and HASIOTIS, S.T., 2006, The identification and interpretation of reptile ichnofossils in paleosols through modern studies: Journal of Sedimentary Research, v. 76, p. 575–588.

HEMBREE, D.I., and HASIOTIS, S. T., 2008, Miocene Vertebrate and Invertebrate Burrows Defining Compound Paleosols in the Pawnee Creek Formation, Colorado, U.S.A: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 270, p. 349–365.

HEMBREE, D.I., HASIOTIS, S.T., and MARTIN, L.D., 2004, Amphibian burrows and ephemeral ponds of the Lower Permian Speiser Shale, Kansas: evidence for seasonality in the midcontinent: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 203, p. 127–152.

HEMBREE, D.I., HASIOTIS, S.T., and MARTIN, L.D., 2005, *Torridorefugium eskridgensis* (new ichnogenus and ichnospecies): Amphibian aestivation burrows from the Lower Permian Speiser Shale of Kansas: Journal of Paleontology, v. 79, p. 583–593.

HUNT, R.M., XIANG-XUE, X., KAUFMAN, J., 1983, Miocene burrows of extinct bear dogs: indication of early denning behavior of large mammalian carnivores: Science, v. 221, p. 354–366.

JARVIS, J.U.M., and SALE, J.B., 1971, Burrowing and burrow patterns of east African mole–rats *Tachyoryctes, Heliophobius, Heterocephalus*: Journal of Zoology London, v. 163, p. 451–479.

KINLAW, A., 1999, A review of burrowing by semi-fossorial vertebrates in arid environments: Journal of Arid Environments, v. 41, p. 127–145.

LOOPE, D.B., 2006, Burrows dug by large vertebrates into rain-moistened Middle Jurassic dunes: The Journal of Geology, v. 114, p. 753–762.

LOOPE, D.B., 2008, Life beneath the surface of active Jurassic dunes: burrows from the Entrada Sandstone of south-central Utah: Palaios, v. 23, p. 411–419.

LUCAS, S.G.., GOBETZ, K.E., ODIER, G.P., MCCORMICK, T., and EGAN, C., 2006, Tetrapod burrows from the Lower Jurassic Navajo Sandstone, Southeastern Utah: New Mexico Museum of Natural History and Science, Bulletin 37, p. 147–154.

MARTIN, L.D., and BENNETT, D.K., 1977, The burrows of the Miocene beaver *Palaeocastor*, western Nebraska, U.S.A: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 22, p. 173–193.

MILLER, M.F., HASIOTIS, S.T., BABOCK, L.E., ISBELL, J.L., and COLLINSON, J.W., 2001, Tetrapod and large burrows of uncertain origin in Triassic high paleolatitude floodplain deposits, Antarctica: Palaios, v. 16, p. 218–232.

OLSON, E.C., and BOLLES, K., 1975, Permo-Carboniferous fresh water burrows: Fieldiana Geology, v. 33, p. 271–290.

ROMER, A.S., and OLSON, E.C., 1954, Aestivation in a Permian lungfish: Breviora, v. 30, p. 1–8.

SMITH, R.M.H., 1987, Helical burrow casts of therapsid origin from the Beaufort Group (Permian) of South Africa: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 60, p. 155–170.

SPINKS, A.C., and BENNETT, N.C., JARVIS, J.U.M., 2000, A comparison of the ecology of two populations of the common mole-rat, *Cryptomys hottentotus hottentotus:* the effect of aridity on food, foraging and body mass: Oecologia, v. 125, p. 341–349.

VOORHIES, M.R., 1974, Fossil pocket mouse burrows in Nebraska: American Midland Naturalist, v. 91, p. 492–498.

VOORHIES, M.R., 1975a, A new genus and species of fossil kangaroo rat and its burrow: Journal of Mammalogy, v. 56, p. 160–176.

VOORHIES, M.R., 1975b, Vertebrate burrows, *in* Frey, R.W. eds., The Study of Trace Fossils, Spring-Verlag, New York, p. 325–350.

CHAPTER TWO. SYNAPSID BURROWS AND ASSOCIATED TRACE FOSSILS IN THE LOWER JURASSIC NAVAJO SANDSTONE, UTAH, INDICATE A WET DESERT ECOSYSTEM

ABSTRACT

Enigmatic structures in the Lower Jurassic Navajo Sandstone near Moab, Utah, occur at three localities below carbonate beds that record interdune lake deposits. These structures are interpreted as mammal and therapsid burrows based on their architectural and surficial burrow morphologies: Type I (large diameter) and Type II (mega diameter) burrows. Type I burrows include sinuous tunnels, Y- and T- branched tunnels, sinuous ramps, and chambers, and weather into mounds averaging 33 m x 22 m and extend ~ 1 m above the surface. Type I burrows are dorsoventrally flattened, in cross section averaging 9.3 cm wide and 4.2 cm high, and are sand filled and structureless. Type I burrows mostly have smooth walls, though some have scalloped walls. Type II burrows are simple, inclined tunnels ~ 35 cm wide and ~ 20 cm high, and exhibit well-preserved bilobate morphology along the underside of the tunnel. The walls preserve a series of 3 or 4 thin (~ 4–8 mm), inclined scratch marks from the upper part of the wall and along the floor. The great complexity and high density of Type I burrow systems is best explained by multiple individuals living together in social groups. These burrows are more complex than Early Triassic therapsid burrows from South Africa and are most similar to burrows of extant social (e.g., voles) and eusocial mammals (e.g., naked mole rats). Type II burrows were likely constructed by therapsids, based on burrow size and comparison to Permian and Triassic therapsid burrows from South Africa and Antarctica.

INTRODUCTION

This paper presents evidence that large-diameter, enigmatic structures in the Lower Jurassic Navajo Sandstone near Moab, Utah, U.S.A., are burrows constructed by synapsids: mammals and therapsids. Morphological criteria developed in this study can be used in future studies to differentiate between biogenic and abiogenic structures in continental deposits with similar morphologies. These structures are enigmatic because of their large size and occurrence in eolian deposits. Researchers have interpreted these structures as rhizoliths, termite nests, concretions, weathering or erosional features, and vertebrate burrows (e.g., Lucas et al. 2006; J.I. Kirkland, personal communication 2008).

The continental fossil record contains few examples of burrows excavated by vertebrates compared to burrows attributed to invertebrates (e.g., Benton 1988; Voorhies 1975a; Hasiotis et al. 2007a). Burrows excavated by vertebrates can be identified based on the preservation of body fossils within the burrows (e.g., Smith 1987; Groenewald et al. 2001) or more commonly from their architectural and surficial morphologies (Hasiotis and Mitchell 1993; Hasiotis et al. 2004; Hasiotis et al. 2007b; Miller et al. 2001). Body fossils found within burrow casts and identified as the excavator include amphibians (Olson and Bolles 1975), lungfish (Romer and Olson 1954; Carlson 1968; Olson and Bolles 1975; Dalquest and Carpenter 1977; Hasiotis et al. 1993), therapsids (Smith 1987; Groenewald et al. 2001; Damiani et al. 2003), bear dogs (Hunt et al. 1983), beavers (Martin and Bennett 1977), and mammals (Voorhies 1974, 1975b). Excavators of vertebrate burrows identified based on architectural and surficial morphologies, include lungfish (Carroll 1965), amphibians (Hembree et al. 2004, 2005), reptiles (Hasiotis et al. 2004; Hembree and Hasiotis 2006), therapsids (Miller et al. 2001; Lucas et al. 2006), rodents (Bown and Kraus 1983; Gobetz 2006; Gobetz and Martin 2006), beavers (Martin and Bennett 1977), and mammals (Hasiotis 2002, 2004; Hasiotis et al. 2004; Hembree and Hasiotis 2008).

Vertebrate burrows are found in nearly every present-day continental environment, including eolian settings (Ahlbrandt et al. 1978; Kinlaw 1999; Hasiotis et al. 2007a). Likewise, fossil vertebrate burrows are commonly found in lithologies representing fluvial floodplain, lacustrine, or palustrine environments (e.g., Smith 1987; Groenewald et al. 2001; Miller et al. 2001; Hasiotis et al. 2004; Hasiotis et al. 2007b). Few structures found in eolian deposits have been interpreted as fossil vertebrate burrows, possibly because geologists are hesitant to interpret large-diameter structures as burrows (e.g., Martin and Bennett 1977; Voorhies 1975a; Ahlbrandt et al. 1978; Gobetz and Martin 2006, Loope 2006a; Loope 2008).

GEOLOGIC SETTING

The Lower Jurassic Navajo Sandstone, part of the Glen Canyon Group, crops out on the Colorado Plateau in southwest U.S.A. (Fig. 1) (Harshbarger et al. 1957). The Navajo Sandstone is only 75–140 m thick in the Moab area (Parrish and Falcon-Lang 2007) compared to its maximum thickness of 700 m in the Utah-Idaho trough (Kocurek 2003). The Navajo Sandstone consists of a lower eolian interval, which intertongues with fluvial deposits of the Kayenta Formation, and an upper entirely eolian interval. Very fine- to medium-grained quartzose sandstone units > 20 m thick (Gilland 1979) are stacked vertically throughout the Navajo Sandstone (Kocurek 2003). Interdune deposits include carbonate mounds and flat-lying carbonate beds deposited by nonbiological precipitates of spring vents and spring-fed lakes (Gilland 1979; Parrish and Falcon-Lang 2007). Interdune deposits can also include planar-bedded to structureless mudstone and sandstone (Eisenberg 2003; Irmis 2005). Lenticular structureless sandstone beds in interdune deposits are interpreted as mass-flow deposits (Parrish and Falcon-Lang 2007).

Figure 1—Location of Navajo Sandstone outcrops in Utah, Arizona, Colorado, and New Mexico. Star = study area near Moab, Utah. Modified from Winkler et al. (1991).

The study area was located ~ 10° N latitude (Loope et al. 2001) within a foreland basin at time of deposition (Kocurek 2003). Annual summer monsoonal rains interpreted from slump deposits in the unit (Loope et al. 2001; Loope et al. 2004b) sustained interdune biota (Winkler et al. 1991; Loope and Rowe 2003).

Biota in the Navajo Sandstone is recognized based on plant, invertebrate, and vertebrate body fossils that include ostracodes, sphenophytes, tritylodontids, theropod dinosaurs, crocodylomorphs, and prosauropods (Winkler et al. 1991; Irmis 2005; Parrish and Falcon-Lang 2007). Trace fossils, however, represent evidence mostly of invertebrates in eolian deposits (e.g., Ahlbrandt et al. 1978; Ekdale and Picard 1985; Tanner et al. 2006; Ekdale et al. 2007; Hasiotis et

al. 2007b; Loope 2008). Ichnotaxa in the Navajo Sandstone likely produced by arthropods include *Planolites beverleyensis*, *Palaeophycus tubularis*, *Skolithos linearis*, *Arenicolites* isp., and *Taenidium serpentinus* (e.g., Loope and Rowe 2003; Loope et al. 2004a; Ekdale et al. 2007). Rhizoliths, large silicified coniferous tree trunks, and stumps record plant life (Loope 1988; Hasiotis et al. 2007b; Parrish and Falcon-Lang 2007). Vertebrate trace fossils include dinosaur and reptile tracks, and burrows in the Navajo Sandstone (Baird 1980; Lockley et al. 1992; Lockley et al. 1998; Lockley and Hunt 1995; Rainforth and Lockley 1996; Loope and Rowe 2003; Irmis 2005; Lockley 2005; Seiler and Chan 2008).

MATERIALS AND METHODS

Enigmatic structures were investigated at four localities ~ 48 km northwest of Moab, Utah, in the vicinity of Canyonlands National Park (Figs. 2, 3). Exact GPS locations are not presented here in order to protect the sites; GPS coordinates are available upon request from the University of Kansas Vertebrate Paleontology Museum. Horizons bearing these structures commonly lack visible bedding.

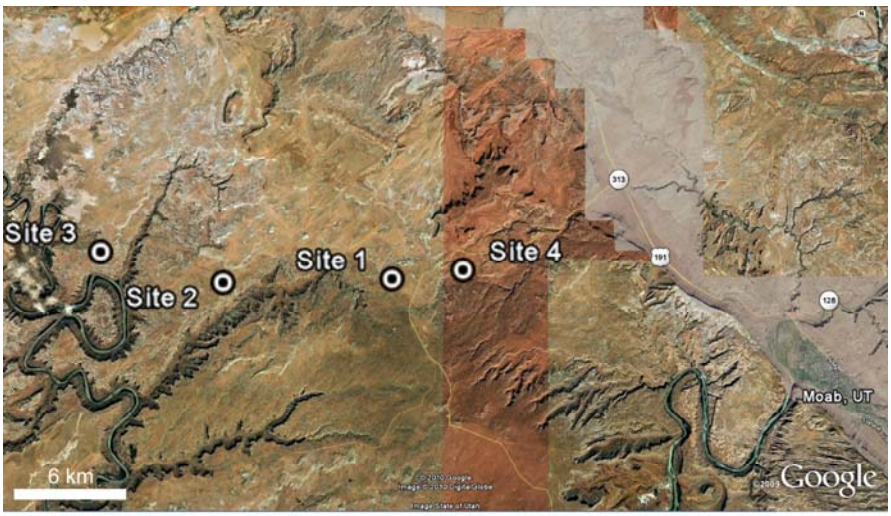

Figure 2—Locations investigated for enigmatic structures. Courtesy of Google Earth.

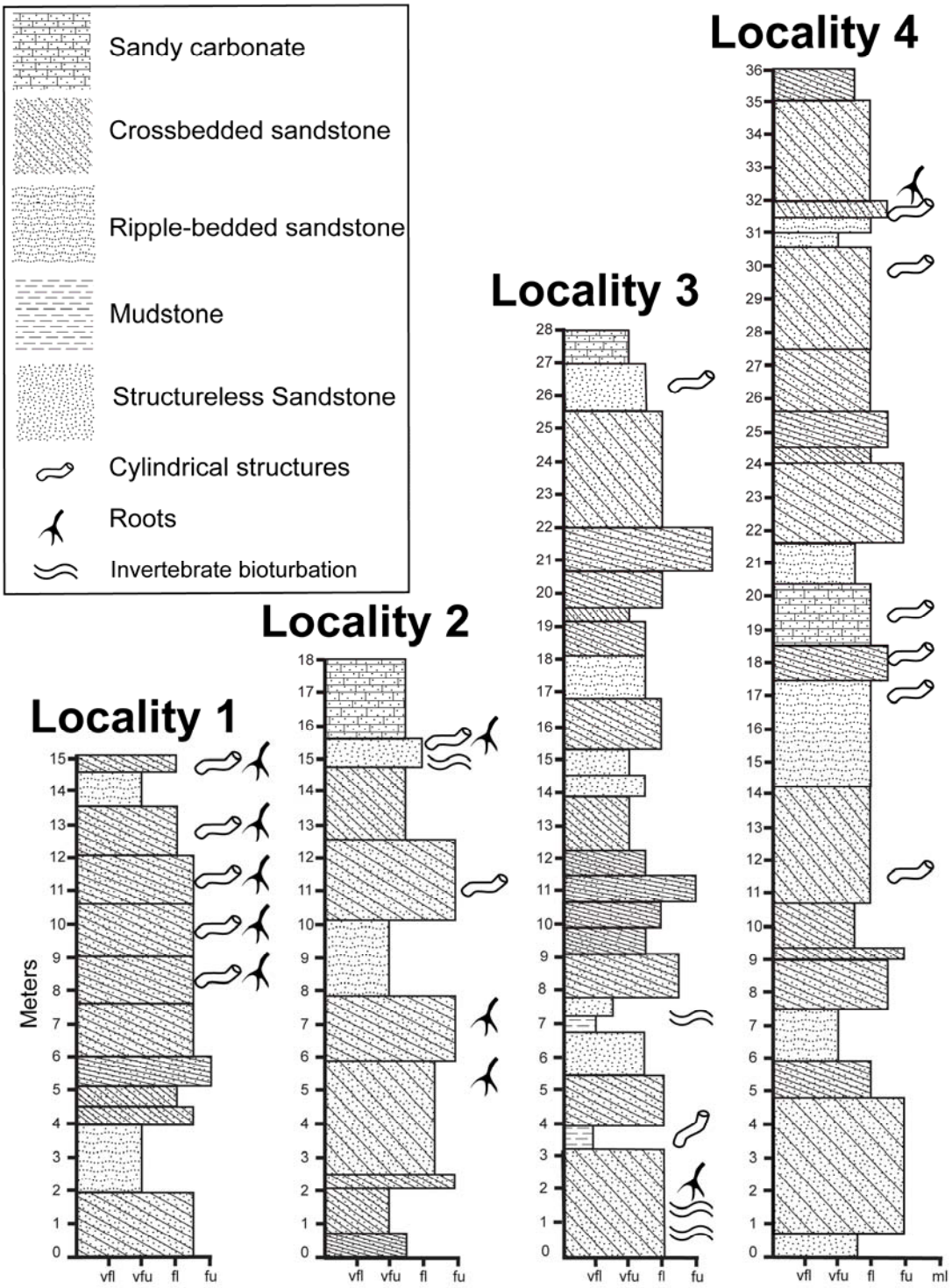

Figure 3—Stratigraphic columns of the four localities investigated. Grain size of sand: vfl = very fine lower; vfu = very fine upper; fl = fine lower; fu = fine upper; ml = medium lower.

Locality 1 is located ~ 32 km northwest of Moab where structures occur in differentially weathered mounded areas separated by cross-bedded sandstone (Fig. 4). Here, structures are in host rock composed of very fine- to fine-grained buff-colored, cross-bedded sandstone. In some areas ripple cross-laminated sandstones is present as well. Locality 2 is located ~ 48 km northwest from Moab and comprises two sites. Structures at one site weather out along a ridge from a horizon ~ 15 m above the base of the Navajo Sandstone (Fig. 5); another site is located ~ 100 m from the ridge. Evidence of invertebrate burrowing underlying interdune deposits was also observed at this locality. Locality 3 is located ~ 57 km northwest from Moab where structures weather out on top of a ridge (Fig. 6). The main structure bearing horizon is ~ 26 m above the base of the Navajo Sandstone, as well as in a brown mudstone interpreted as interdune near the base. An exceptionally well-preserved structure, weathering out of mudstone, occurs ~ 3.5 m above the base of the Navajo Sandstone. A sandy carbonate bed is present above the enigmatic structures, ~ 27 m above the base of the Navajo Sandstone. Locality 4 is located ~ 30 km northwest from Moab and comprised three sites where structures weather out along a ridge ~ 30 m above the base of the Navajo Sandstone (Fig. 7). A few structures occur at ~ 12 m, and 17–20 m above the base. Rhizoliths are dominant at this locality. Some sites at localities 2–4 directly underlie interdune deposits composed predominantly of gray sandy carbonate. Rhizoliths and invertebrate trace fossils were found in association with the structures at all localities.

Sedimentary facies were described and stratigraphic columns constructed for each locality. Stratigraphic sections were measured from the base of the Navajo Sandstone and measured up to a few meters above the highest horizon of structures. The strata were also explored for body fossils and tracks, particularly in association with the structures and in

interdune deposits. A section was not measured from the base of the Navajo Sandstone at locality 1 in as much as it is only a surface exposure.

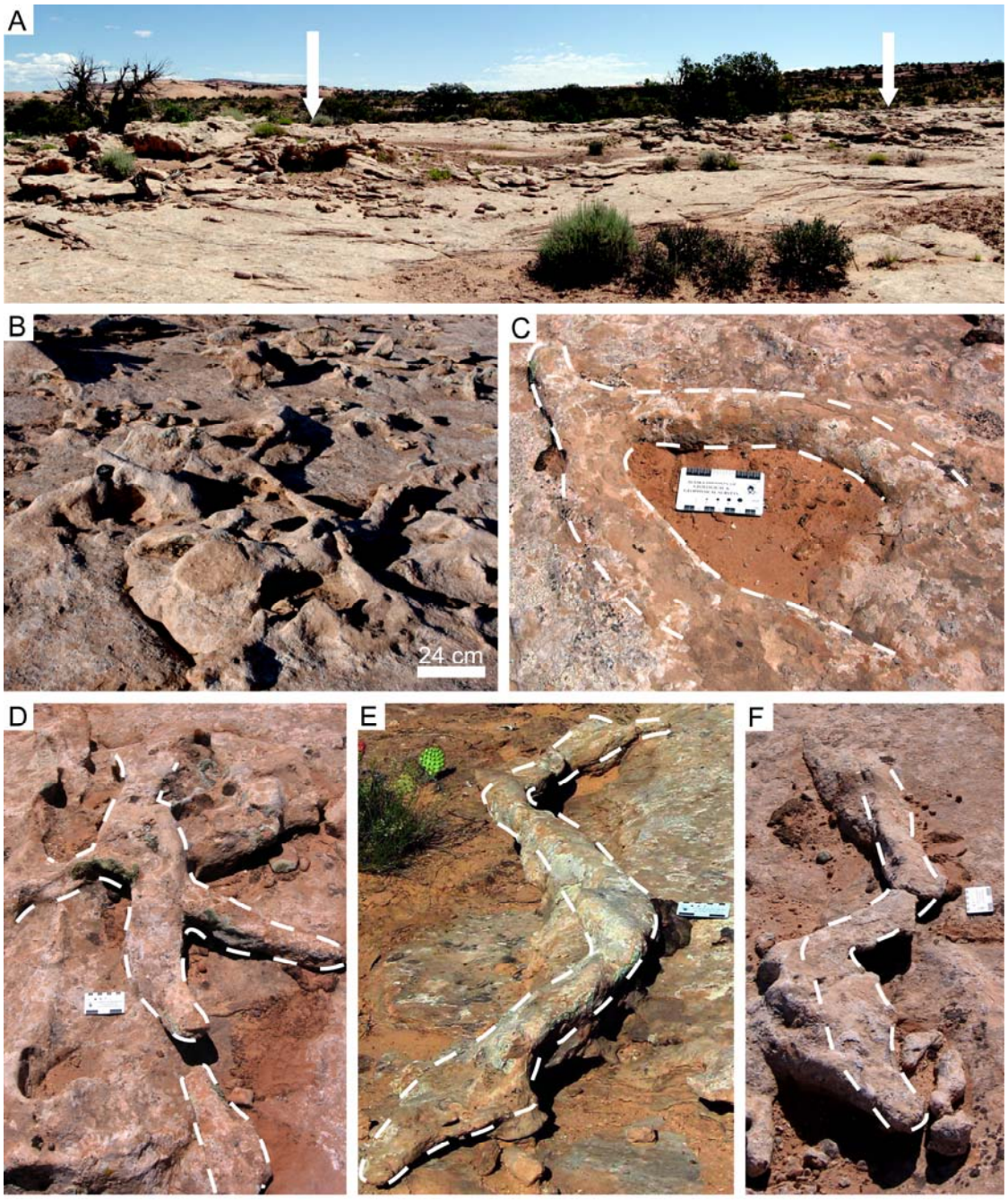

Figure 4—Locality 1. A) Panorama of locality. B) Interconnecting elements in a complex network. C) Y-branching. D) Multiple branches. E) Sinuous architecture. F) Sinuous architecture. Black or white bar on scale = 1 cm.

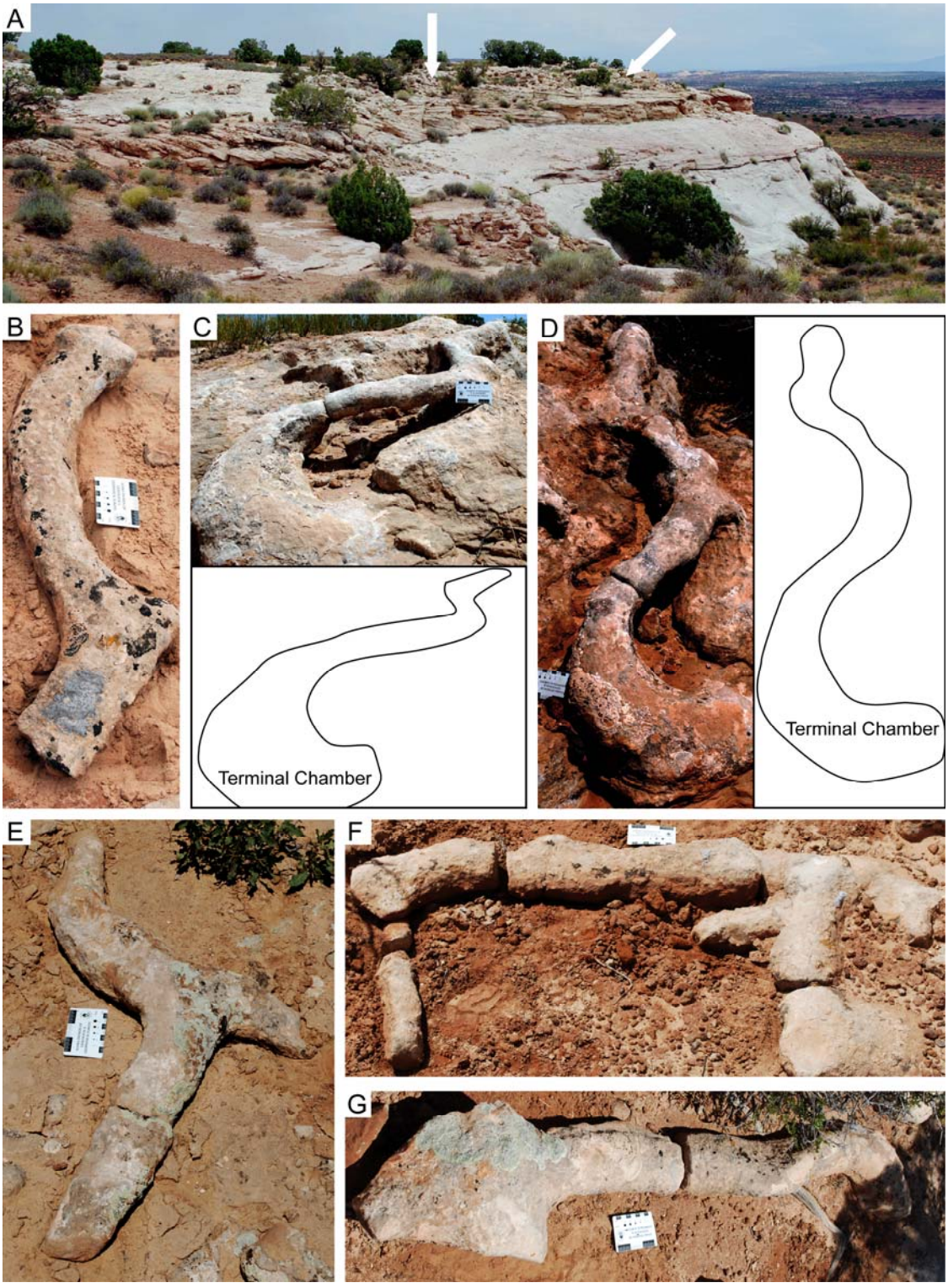

Figure 5—Locality 2. A) Navajo Sandstone bluff. B) Slight curve and a bend in an element. C) Cross section of sinuous architecture crosscutting bedding. D) Plan view of structure in part C with sinuous architecture. E) T-branching and slight curve. F) Right-angle bend. G) Straight element leading to an enlarged area. Black or white bar on scale = 1 cm.

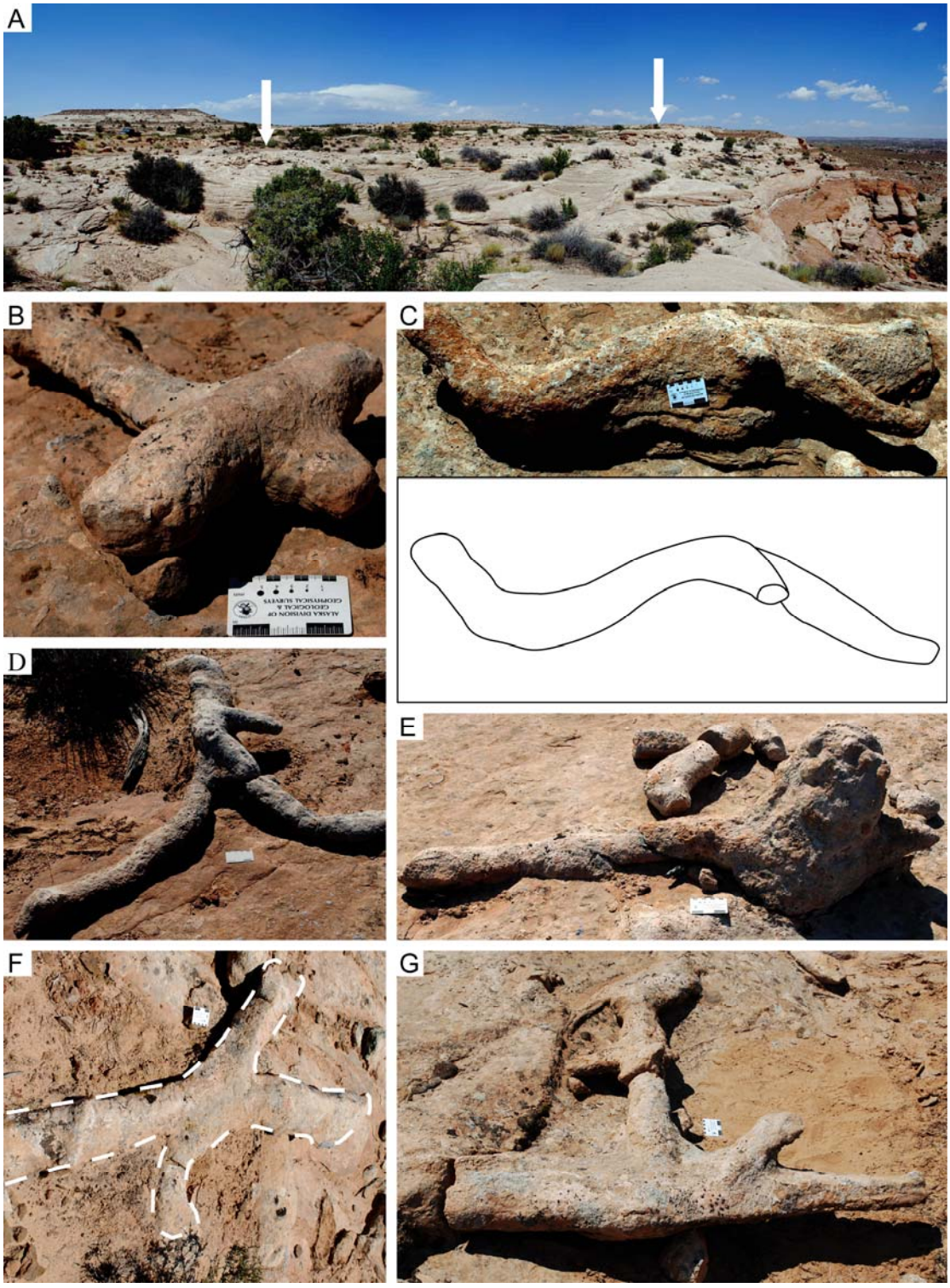

Figure 6—Locality 3. A) Panorama showing area where enigmatic structures were located. Elements with various morphologies include B) T-branching. C) Sinuous architecture. D) Outward branching from structure. E) Enlarged area with outward-branching element. F) Y-branching. G) T- and Y-branching. Black or white bar on scale = 1 cm.

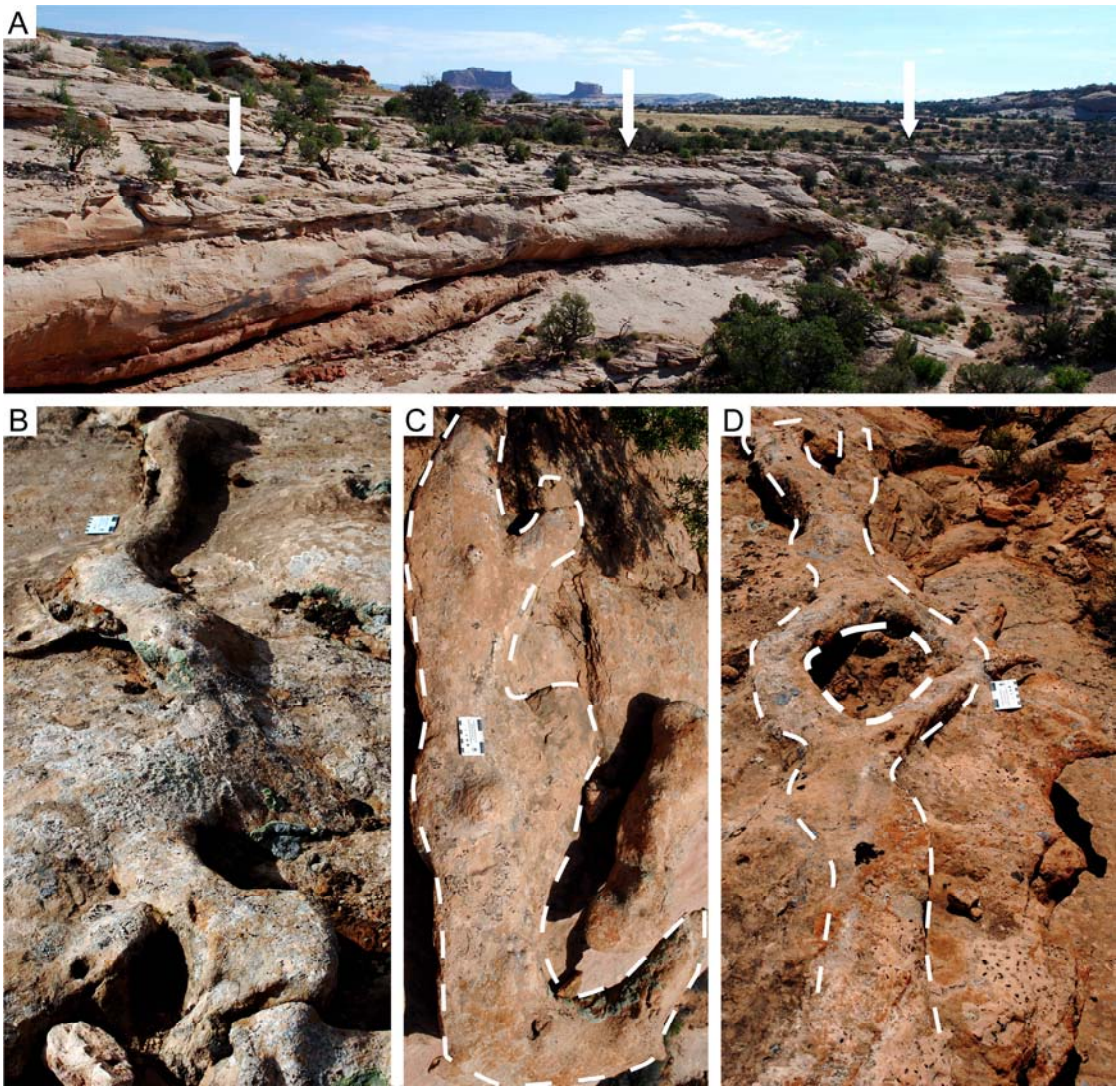

Figure 7—Locality 4. A) Area where enigmatic structures are located, with various morphologies. B) Sinuous architecture. C) Y-branching and curving. D) Y-branching intersection. Black or white bar on scale = 1 cm.

Architectural and surficial burrow morphologies were used to describe and measure the structures (Appendix 1), which were photographed in detail. Architectural morphology comprises width, height, and length of individual elements between branched portions of the structures, as well as the angles of branching and inclination from the horizontal. Measurements were taken using a measuring tape and calipers. Surficial morphology comprises patterns on the

walls of the structures, including scalloped features and longitudinal ridges, of which the length, width, and position was recorded. Petrographic thin sections were made from enigmatic structures, host rock, carbonate beds, and rhizoliths. Thin sections were studied to aid in description and identification of lithologies of associated trace fossils.

A database was constructed with quantitative descriptions of architectural and surficial morphologies of the enigmatic structures from the Navajo Sandstone (Appendix 1). This database was compared to qualitative and quantitative descriptions of structures produced by modern plant roots, fluid-escape structures, wind-sculpted rock, and modern and ancient vertebrates, compiled from ongoing field investigations and from the literature (Table 1).

ANALYSIS OF ENIGMATIC STRUCTURES

There are two major types of architectural morphologies. The more abundant are referred to as Type I, and the less abundant are referred to as Type II. All structures are infilled with fine-grained sand and show no internal structure or lining around the perimeter. Petrographic analysis shows that the sandstone within the structures was cemented mainly by quartz overgrowths. No skeletal elements were found during the course of this study.

Table 1—Summary of biogenic and abiogenic architectural and surficial morphologies.

		Architectural Morphology	Orientation	Cross Section	Branching	Surficial Morphology	Other	References
Mammal Burrows		Long branching tunnels composed of primary shafts and laterals; spiral tunnels	Random orientation	Elliptical to nearly cylindrical burrows	Simple to complex branching pattern	Incisor or claw marks on walls reflecting the digging apparatus	Bilobate terminus	Hasiotis et al., 2004; Gobetz, 2006; Gobetz and Martin 2006
Therapsid Burrows		Inclined entry and terminal chambers connected by helical spiral	Shallowly inclined, spiral	Flattened biconvex shape; elliptical	Branching present; terminal chamber present	Chevrons of narrow ridges on tops and sides interpreted as scratch marks	Diameter 6-25 cm	Smith, 1987; Groenewald et. al., 2001; Miller et al.,2001; Hasiotis et al., 2004
Reptile Burrows	**Skink**	Interconnected, inclined tunnels and switchbacks; elliptical, straight to curved tunnels	horizontal and vertical	elliptical	5-10 segments	Longitudinal median groove, scalloped walls	Terminal chamber absent	Hasiotis et al., 2004; Hasiotis and Bourke, 2006; Hembree and Hasiotis, 2006
	Amphisbaena	Complex, interconnected networks; multiple branches per junction; cylindrical, sinuous to straight tunnels	horizontal and vertical	circular to ovoid	20-30 segments	Triangular impressions on tops and sides of tunnels	Terminal chamber absent	
Rhizoliths		Downward bifurcations with decreasing diameters of branches from main system; similar diameters; dendritic pattern; rectilinear	Show many orientations but horizontal and vertical are most common; orientation may be parallel to lamination or parallel to dip direction	Circular	Branching tubes filled by materials (sand, clay), or with root	Distinctive fabric from surrounding matrix	Distinctive geochemical compositions and petrographic characteristics from surrounding matrix	Klappa, 1980; Loope, 1988; Hasiotis, 2002; Krauss and Hasiotis, 2006
Fluid-Escape Pipes		Nearly vertical pillar-like structures which cut across host rock; distinct boundaries with respect to undisturbed wind-deposited sand	Lateral contact of massive or slumped sandstone, nearly vertical, though some display toungue-like bodies	Internal structure: Pipes can be massive, but typically cone-shaped, concentric sediment layers	No branching present	pipes may contain breccia blocks; external features show flow structures	Relatively homogeneous; smallest pipes range 4 to 200 mm in diameter, large pipes 1 to > 4 m in diameter	Netoff, 2002; Huuse et al., 2005; Hasiotis et al., 2007
Eroded-Rock Remnants		No preferred morphology	Towards or parallel to strong winds	no preferred shape	no preferred branching	Smoothing and polishing of rock surfaces; etching; flutes and grooves	Primary sedimentary structures preserved	Lancaster, 1984

Type I Structures

Architectural Morphology.—Type I comprise high-density, complex networks of interconnected Y- and T- branched, inclined ramps, horizontal to subhorizontal large-diameter elements (i.e., structures) preserved as differentially weathered low relief mounds (Figs. 4–7) (Appendix 1). The mounded areas show elements that are topographically higher than elements on the periphery and the surrounding rock. Mounds are circular to elliptical in plan view and range from 40 m x 40 m to 10 m x 15 m and are ~ 1 m high (avg. 33 m x 22 m, ~ 1 m in height), which are not always apparent when pervasive over the entire outcrop (Fig 8).

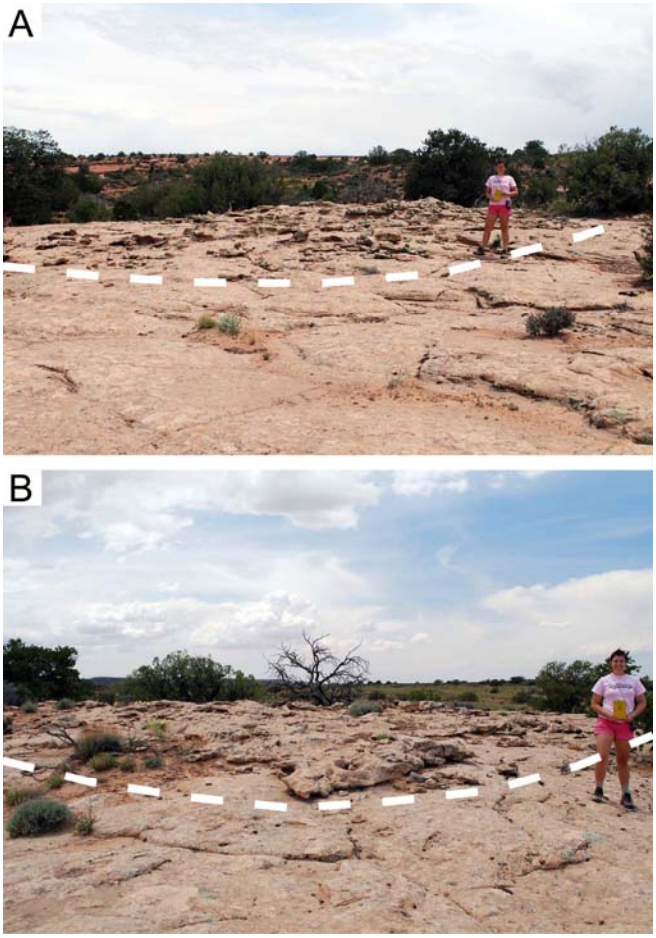

Figure 8—Mound structures at locality 1. Person for scale 5′6″.

Individual elements weather out in three-dimensional relief and are often found in place where they are predominantly horizontal to subhorizontal and weakly sinuous (Figs. 4C, 5C, 6C, 7B). Sinuous elements are also associated with widened terminations (Fig. 5C–D). The angle of inclination from horizontal ranges from 6 to 60º (avg. 24º). Elements are dorsoventrally flattened and range from 4.2 to 21 cm in diameter (avg. 9.3 cm) and from 1.2 to 10.2 cm high (avg. 4.2 cm) (Appendix 1; Fig. 9), and the average width-to-height ratio is 2.2 (Fig. 10). The floor of most elements is predominantly flat, whereas the top surface is curved. Elements are interconnected to form Y- and T-branched intersections, 40–160º (avg. 97º) and ~ 90º angles, respectively, and are commonly wider than the diameter of intersecting elements (Figs. 4D, 6B).

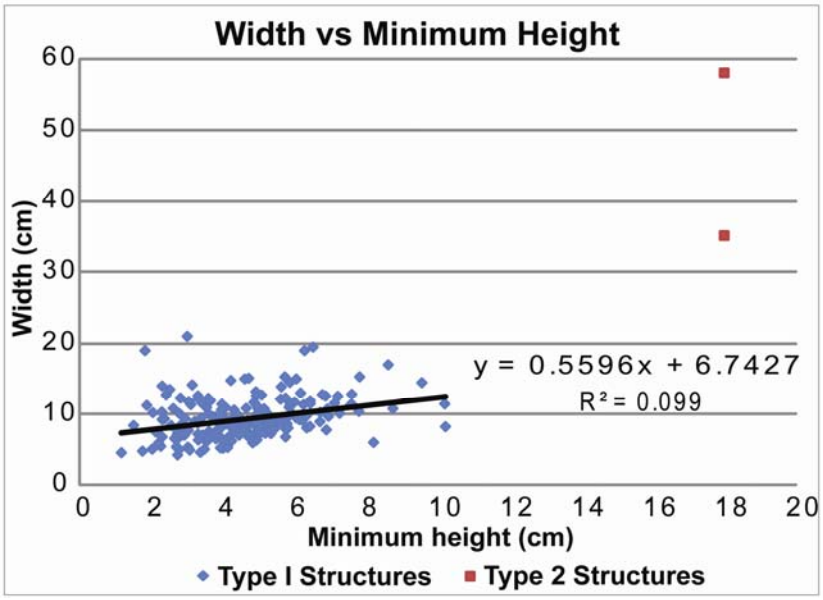

Figure 9—Scatter plot of width vs. height of elements.

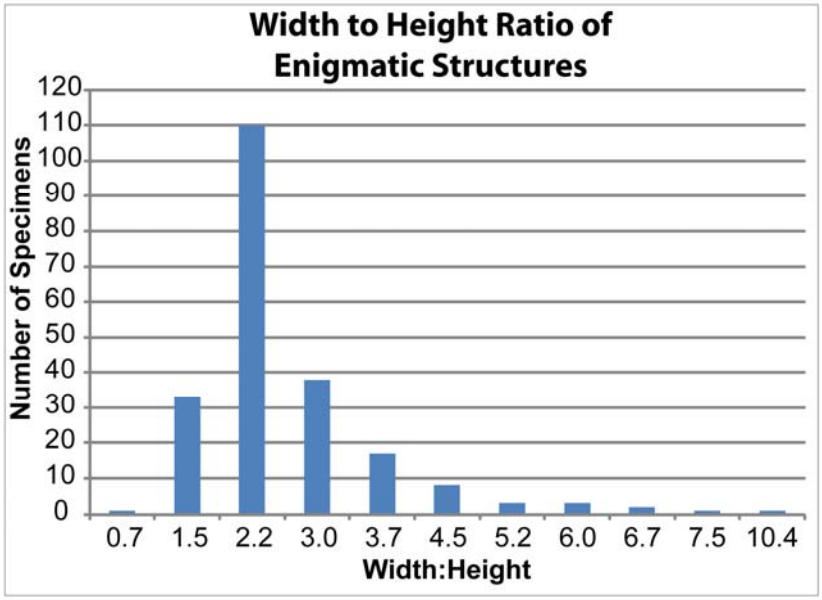

Figure 10—Histogram of width-to-height ratio of elements.

Surficial Morphology.—Smooth walls dominate these elements (Fig. 11A). Some exhibit scalloped features paired along the outer edge (Fig. 11C). Widths of scallops range from 5 to 7 cm (avg. 6.4 cm), and protrude outward 0.5–1.5 cm (avg. 1 cm) (Appendix 1). The walls also show evidence of rhizoliths and small-diameter, passively filled burrows (Fig. 11B).

Type II Structures

Architectural Morphology.—Type II comprise dorsoventrally flattened structures. The first is 35 cm wide 18 cm high, and ~ 6.17 m long, extending from a sandstone bed into the underlying mudstone at a 25° angle (Fig. 12A). The portion in sandstone is poorly preserved for ~ 4 m as a weathered ledge with mud clasts for ~ 4 m. The portion in mudstone is well preserved for ~ 2.2 m and curves into the outcrop and out of view. In the mudstone this structure has a raised floor 20–25 cm wide (from the center of each lobe) and 2–2.5 cm high (from the base of

the lobe to the height of the raised floor), creating a bilobate morphology (Fig. 12B). Each lobe is ~ 15–20 cm wide. The second structure, 58 cm wide and 18 cm high, is seen in cross section in the mudstone (Fig. 9). It has massive sandstone fill with mud clasts on the perimeter (Fig. 12D).

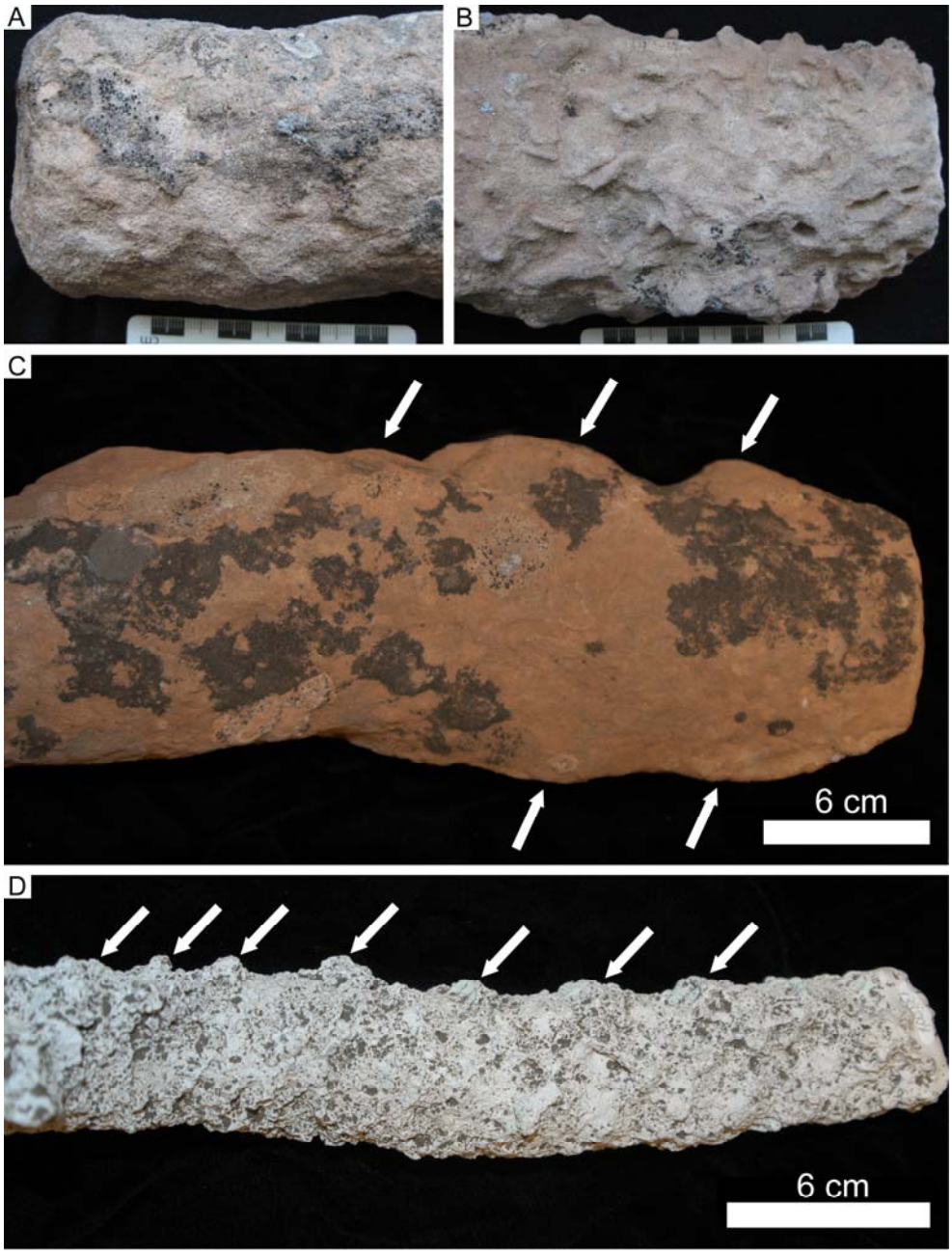

FIGURE 11—Surficial morphology of Type I structures. A) Smooth wall. B) Invertebrate bioturbation seen on a wall. C) Scallops (arrows). D) Extant mole burrow cast with scallops (arrows). Black or white bar on scale = 1 cm.

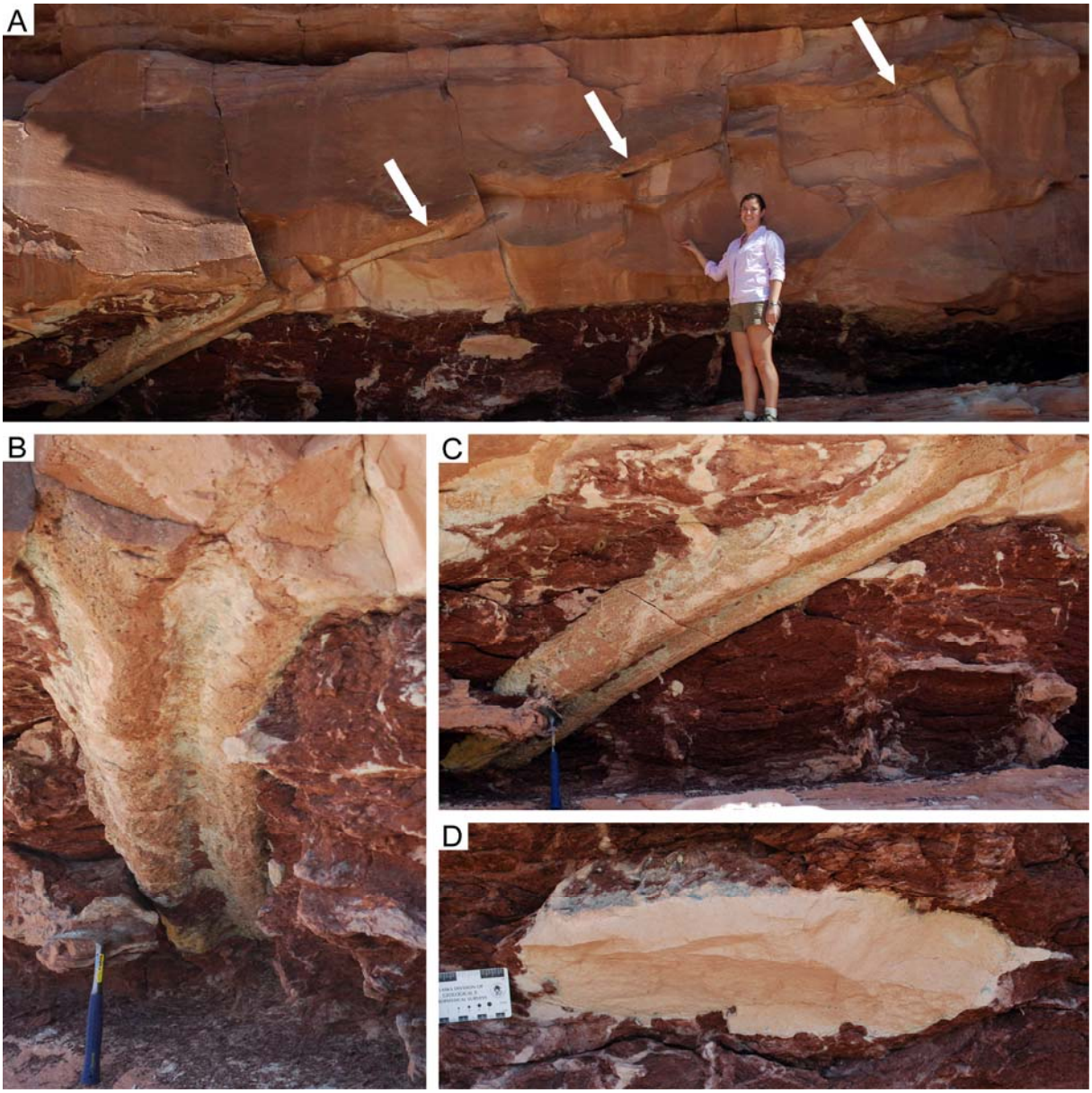

Figure 12—Type II structures. A) Structure in a cross-bedded sandstone extending into mudstone. B) Raised floor creates a bilobate morphology. C) Oblique view of structures in outcrop. Hammer 33 cm. D) Cross-section view. Black or white bar on scale = 1 cm.

Surficial Morphology.—Sets of two or three inclined, parallel longitudinal ridges 4.0–8.0 mm wide (avg. 5 mm) and 2.5–20 cm long (avg. 8.8 cm) extend from the upper part of the wall and along the floor of the structure (Fig. 13). Distance ranges between each ridge from 1.5 to 3 cm (avg. 2.3 cm). Ridges from the upper part of the wall are inclined from 14° to 30° (avg. 23.2°). Ridges on the base of the floor are 6–11 mm wide (avg. 9 mm) and 3–18.5 cm long (avg. 9.8

cm); distances between each ranges from 1.3 to 3.5 cm (avg. 2.6 cm) (Appendix 1). Ridges converge towards the midline at < 10°, but one ridge crosscut others at a 30° angle.

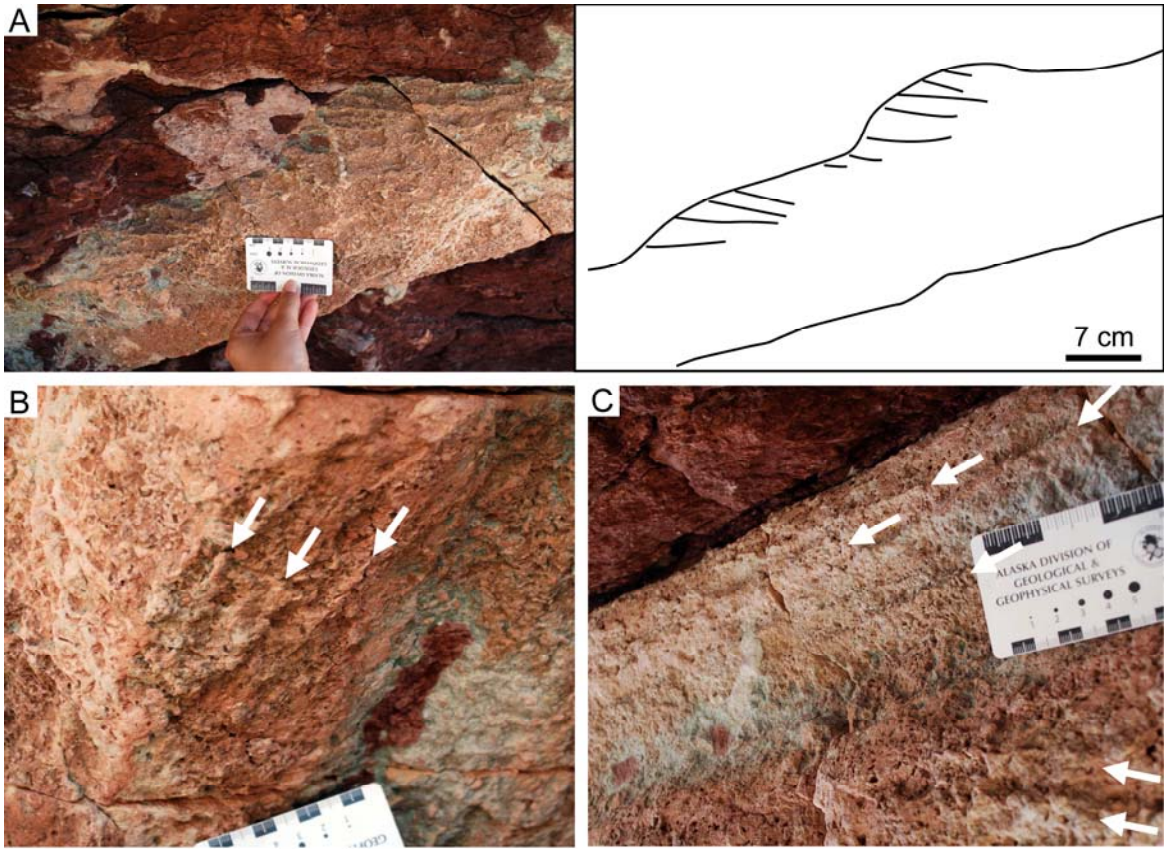

Figure 13—Surficial morphology of Type II structures. A) Parallel ridges on the upper part of the wall, and line drawing of ridge location. B) Three parallel ridges on the lobes (arrows). C) Multiple ridges on the lobe (arrows). Black or white bar on scale = 1 cm.

INTERPRETATION OF ENIGMATIC STRUCTURES

Type I Structures

Architectural Morphology.—Type I elements and mound features are comparable with large complex burrow systems and mounds produced by social and eusocial mammals that show interconnected, sinuous, and multiple branching tunnels and ramps. Such modern fossorial social

(prairie dogs, voles) and eusocial (naked mole rats) mammals excavate large complex burrow systems that include many interconnected long and short tunnels that lead to chambers used for foraging, nesting, reproduction, defecation, or escape from predators (Figs. 14, 15) (e.g., Jarvis and Sale 1971; Davies and Jarvis 1986; Burns et al. 1989; Reichman and Smith 1990; Hickman 1990; Kinlaw 1999; Nevo 1999; Herbst and Bennett 2006).

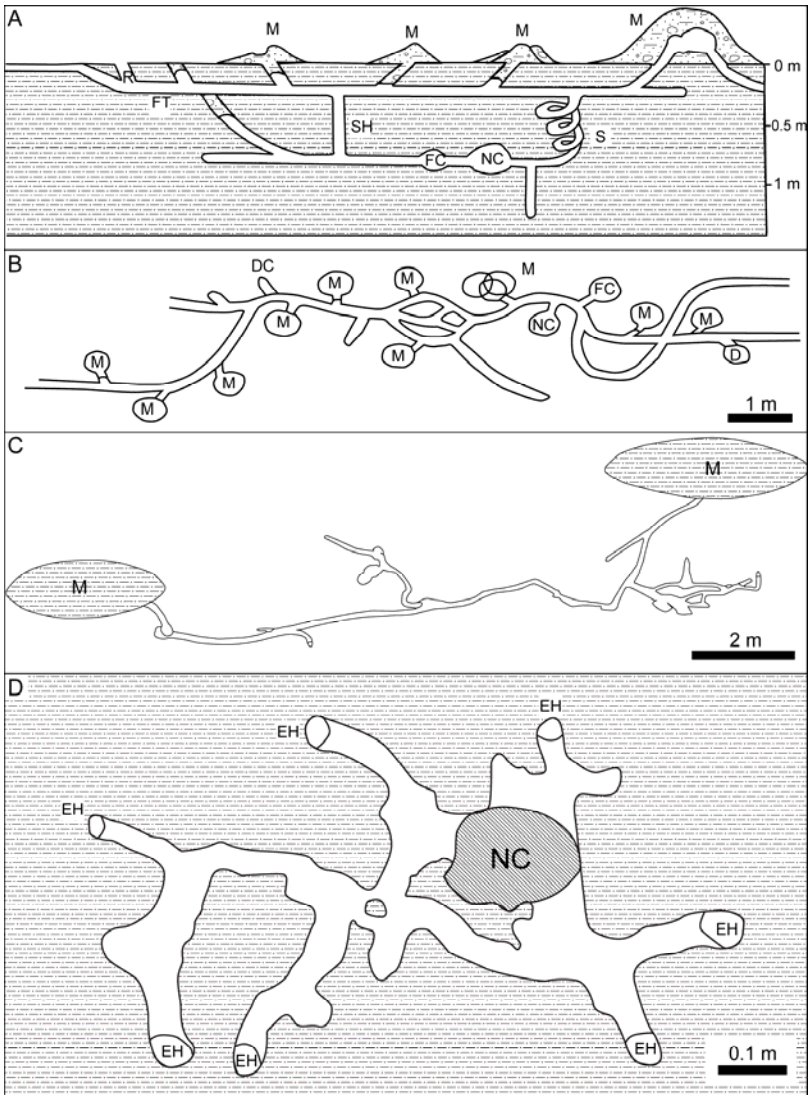

FIGURE 14—Architecture of mammal burrows. M = mound; R = ramp; FT = foraging tunnel; SH = shaft; FC = food chamber; NC = nest chamber; S = spiral ramp; DC = defecation chamber; EH = entrance hole; D = detritus. A, B) Summary of mammal burrow architectures. Enlarged areas are chambers. Modified from Hickman (1990). C) Plan view of prairie-dog burrow system. Modified from Burns et al. (1989). D) Plan view of a communal vole burrow system. Modified from Mankin and Getz (1994).

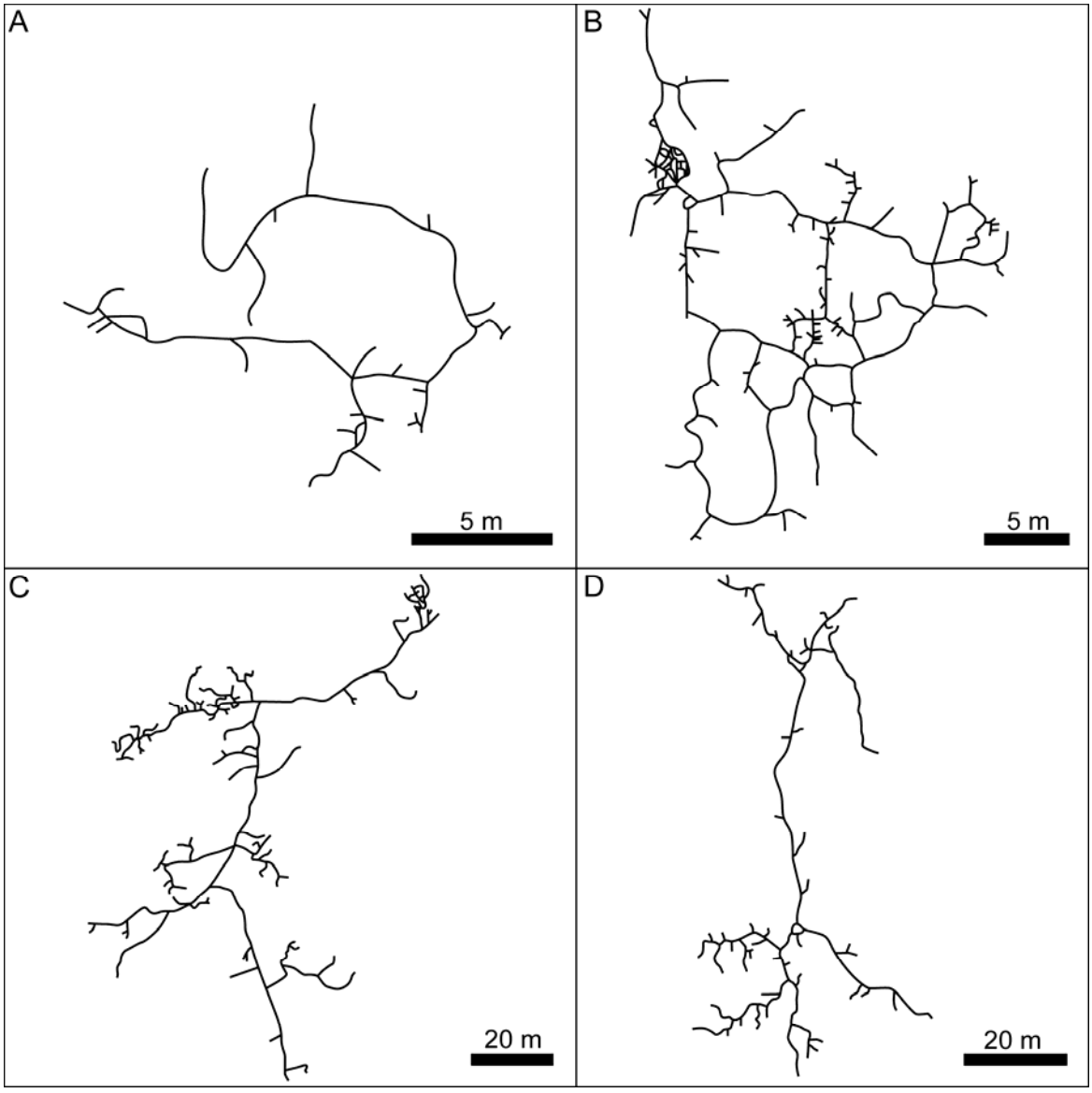

Figure 15—Mole-rat burrow systems. A, B) Plan view of *Cryptomys hottentotus hottentotus* burrow system at a mesic site. C, D) Plan view of *C. hottentotus hottentotus* burrow system at an arid site. Redrawn from Spinks et al. (2000).

Tunnels and shafts of mammal burrows are cylindrical or ellipsoidal in cross section owing to the dorsoventrally flattened shape of the excavator (Voorhies 1974, 1975b; Smith 1948; Mankin and Getz 1994; Gobetz 2005, 2006; Gobetz and Martin 2006; Hasiotis, unpublished data). Tunnels and shafts often vary in diameter along their length because of multiple

individuals of different ages and sizes, as well as different uses — one-way or two-way traffic, temporary storage, or congregation areas — for the burrows in different places within the burrow system (e.g., Burns et al. 1989; Spinks et al. 2000; Begall and Gallardo 2000; Hasiotis et al., unpublished data). Mammal burrows generally contain lateral tunnels that connect to the surface at angles of ~ 10–45°, horizontal foraging tunnels as a major portion of the burrow system, and tunnels that lead to other tunnels and chambers. Elements can be steep to vertical (shafts ~ 45–90°), gradual inclines (ramps ~ 1–44°), or helical (spiral ramp) (Vleck 1981; Hickman 1990, Hasiotis et al. 2007a) (Fig. 14A). Chambers are commonly spheroidal and larger in diameter than tunnels (Jarvis and Sale 1971; Hickman 1990) (Fig. 14B–D).

During burrow construction, mammals dispose of soil on the surface through the lateral tunnels, creating mounds of various sizes (e.g., Smith 1948; Jarvis and Sale 1971; Davies and Jarvis 1986; Burns et al. 1989; Hickman 1990; Nowak 1991; Herbst and Bennett 2006; Schmeisser et al. 2009). Mima mounds are circular to oval, a few meters to 50 m in diameter, and a few centimeters to 2 m high. These mounds have an enigmatic origin; one hypothesis for their origin is the excavation of soils by subterranean mammals (Dalquest and Scheffer 1942; Cox 1984; Hickman 1990; Lovegrove 1991; Horwath and Johnson 2006).

Surficial Morphology.—A few specimens of Type I burrows exhibit scalloped walls (Fig. 11C) similar to those of other mammalian burrows. Rodent burrows in the Miocene of northeastern Colorado show scallop marks (Gobetz 2006) on the walls of the burrows created by the organism's hand (Gobetz 2006). Scallop marks are found on modern mole burrows, and the shape of the impressions of the walls matches the fingers of the manus on the mole (Fig. 11D). Scallop marks usually occur at regularly spaced intervals and likely represent the excavation motions of the vertebrate pushing its claws into the sediment (Gobetz 2005).

Interpretation of Behavior and Tracemaker.—Type I burrows likely represent the work of multiple individuals, judging by the overall size and complexity of the burrow systems. They were likely permanent dwellings used for a variety of behaviors, including foraging, nesting, hiding, and food storage for a fossorial organism. Permanent dwellings for mammals generally have greater complexity, whereas temporary shelters have less complexity (Vleck 1981; Reichman and Smith 1990; Groenewald et al. 2001). Complex burrow architectures result from multiple individuals in a social or eusocial system (Fig. 15), and are also found in areas with limited food supply (Jarvis and Sale; 1971; Davies and Jarvis 1986; Jarvis and Bennett 1991; Jarvis et al. 1994; Mankin and Getz 1994; Spinks et al. 2000). Complex burrows also aid in escape from predators through the use of multiple entrances and exits and bolt holes—tunnels used to enter a burrow when pursued (Jarvis and Sale 1971; Benton 1988; Kinlaw 1999). The Type I burrows, therefore, are assigned to the behavioral category of polychresichnia because the architecture represents simultaneous, multiple behaviors and uses (Hasiotis 2003).

Type I burrows were most likely excavated by social to eusocial mammals. Although no mammal body fossils have been found in the Navajo Sandstone, at least 8 (McKenna and Bell 1997) to 13 (Kielan-Jaworowska et al. 2004) mammal lineages (at the order or family level) are present by the Late Jurassic—depending on the classification scheme used. Several possible lineages and one taxon that are not clearly mammalian are also recognized in deposits of North America (Jenkins et al. 1983; Lucas and Hunt 1990; Kielan-Jaworowska et al. 2004).

Four major mammal lineages were present by the Early Jurassic (Kielan-Jaworowska et al. 2004). Members of the morganucodonta from the Lower Jurassic Kayenta Formation in northern Arizona comprise the taxa *Dinnetherium nezorum*, a *Morganucodon* species, and a possible haramiyid represented by a single molariform tooth (Jenkins et al. 1983; Kielan-

Jaworowska et al. 2004). Morganucodontans are found in the La Boca Formation in northern Mexico and comprise a taxon similar to *Dinnetherium* (Clark et al. 1994). Postcranial fossils are limited, but suggest that they were the size of a shrew to a rat (skull length 2.7–3.8 cm) (Jenkins and Parrington 1976; Luo et al. 2001; Kielan-Jaworowska et al. 2004).

Several skeletal elements were also found in the La Boca Formation, including a triconodont molar similar to molars of two taxa of the eutriconodonta. Eurticonodontans are known from the Middle Jurassic to the Early Cretaceous, with a possible specimen from the Lower Jurassic of India (Kielan-Jaworowska et al. 2004). Eutriconodontans were some of the largest mammals during the Mesozoic (Kielan-Jaworowska et al. 2004) ranging in body size from ~ 4.4 cm long (*Jeholdens jenkinsi*; Late Jurassic insectivores) to 36 cm long (*Gobicondodon ostromi*; Early Cretaceous carnivore) with a skull length ranging 2.2 to 10 cm long, respectively. Estimation of body size did not include the tail and was based on a reconstruction from Ji et al. (1999) and Jenkins and Schaff (1988). The Early Cretaceous example is comparable in body size to the North American opossum, but with a more robust skeleton. The skeleton that would likely have been the correct size to fit the Type I burrows is a morganucodontan with a skull length ~ 3.8 cm long with a possible body length of ~ 25 cm: the body size of a rat.

Type I burrows are less likely to have been constructed by therapsids, based on the known record of therapsid burrow morphologies in Permian-Triassic deposits (Smith 1987; Groenewald et al. 2001; Miller et al. 2001; Damiani et al. 2003). A body fossil of the therapsid originally described as *Kayentatherium* is known from the Navajo Sandstone in northern Arizona (Winkler et al. 1991); however, it is too large to have produced these burrows.

Type II Structures

Architectural Morphology.—Type II structures compare best with therapsid burrows, based on their simple architecture, burrow diameter, and raised floor. Therapsid burrows (Fig. 16) often comprise horizontal to subhorizontal, helical, curving, and simple branching tunnels that may lead to an enlarged chamber (Smith 1987; Groenewald et al. 2001; Miller et al. 2001; Hasiotis et al. 2004). Therapsids and mammals share similar elements in burrow architecture; however, therapsid burrows are distinguished by being less complex and less interconnected. Therapsid burrows (Fig. 16B, C) are weakly to strongly elliptical in cross section (Smith 1987; Groenewald et al. 2001; Miller et al. 2001), and some have a raised floor that creates a bilobate morphology (Groenewald et al. 2001; Miller et al. 2001; Damiani et al. 2003).

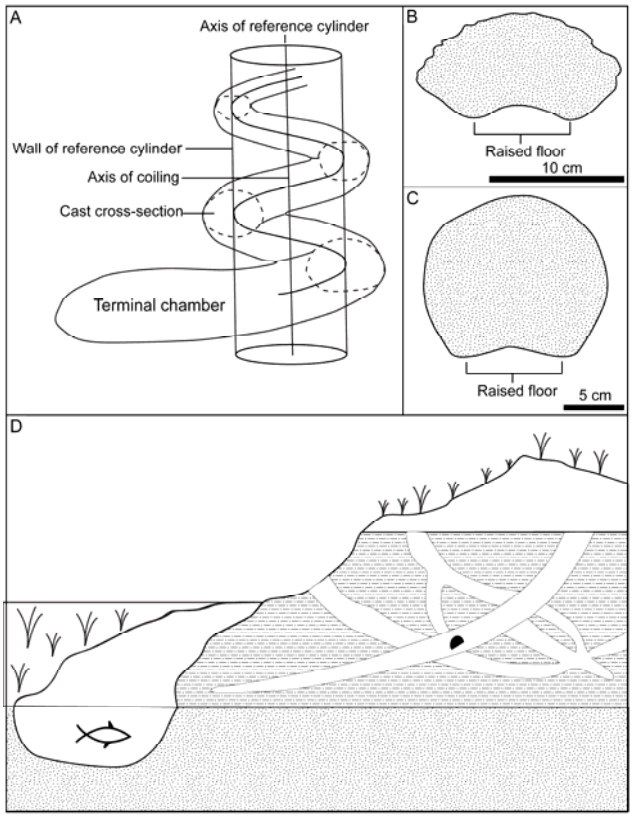

Figure 16—Architectural morphology of therapsid burrows. A) Helical burrow excavated by *Diictodon*. Redrawn from Smith (1987). B) Cross section of an elliptical burrow cast excavated by *Trirachodon* with raised floor. C) Cross section of a circular burrow cast excavated by *Thrinaxodon* with a raised floor. Modified from Damiani et al. (2003). D) Paleoenvironmental

reconstruction of the *Trirachodon* burrow. Parts B and D are modified from Groenewald et al. (2001).

Type II burrows share many similarities in architecture with those of reptiles. Adult crocodiles and alligators generally excavate long, gently dipping tunnels leading to an enlarged den (Voorhies 1975a; Hasiotis et al. 2004). Alligators also dig complex burrows that have numerous tunnels with wet and dry chambers (Zug et al. 2001). The monitor lizard *Varanus mertensi* also constructs a single upward-sloping burrow with no branching, and the tunnel is often straight but sometimes curves to a single terminal chamber. Other species of monitor lizards (e.g., *V. salvator, V. komodoensis,* and *V. griseus*) have more complex burrows with branching and multiple chambers (Mayes 2007). Tunnels of modern skink burrows show a bilobate morphology created from one full-size individual (Hasiotis et al. 2004; Hasiotis and Bourke 2006; Hembree and Hasiotis 2006).

Surficial Morphology.—Parallel longitudinal ridges resemble scratch marks on mammal and therapsid burrows (Martin and Bennett 1971; Smith 1987; Groenewald et al. 2001; Damiani et al. 2003; Hasiotis et al. 2004; Gobetz 2005, 2006; Gobetz and Martin 2006). Scratch marks on mammal and therapsid burrows often are chevron shaped, or parallel sets of 2–4 scratches on the sides and bottoms of burrow walls created from the claws, beaks, or incisors. The claws of the tracemaker likely produced the scratch marks on the Type II burrow walls.

Interpretation of Behavior and Tracemaker.—Type II burrows are problematic to determine because of limited preservation and exposure. The burrow length and bilobate morphology suggests daily use by the organism, and the organism may have sought the more stable interdune mud to produce its nest chamber. These burrows likely represent a permanent dwelling and brooding (i.e., reproduction) structure. Present-day examples of analogous behaviors include alligators, crocodiles, monitor lizards, and such mammals as the platypus,

armadillo, and aardwolf. These organisms spend part of their time in burrows for protection and often construct simple, sometimes linear tunnels that may have an enlarged terminal chamber (Voorhies 1975a; Reichman and Smith 1990; Hasiotis et al. 2004; Anderson and Richardson 2005).

Type II burrows were likely excavated by a large tritylodontid therapsid. A skeleton of a tritylodontid therapsid was found in the Navajo Sandstone in northern Arizona in interdune deposits assigned to *Kayentatherium*, which had a sprawling stance (Winkler et al. 1991). Sues et al. (1994), however, found no diagnostic mammal characters in the specimen and regarded it as a mammalian cynodont of the Tritylodontidae. Sues (1984) hypothesized that tritylodontids were scratch diggers, on the basis of large olecranon process, which resembles such extant scratch-digging mammals as the Mediterranean mole rat (Hildebrand 1974; Winkler et al. 1991).

Several more tritylodontid specimens were found in a sequence of intercalated claystone, sandstone, and siltstone deposits of the Kayenta Formation in northern Arizona (Kermack 1982; Sues 1985, 1986a, 1986b). Many specimens were incomplete, and studies focused on the dentition rather than postcranial material; therefore, skull lengths were given for a size reference. Skull length may relate to total body size: for example *Oligokyphus major* has a skull length of ~ 9 cm and a body size of ~ 50 cm including the tail (Kühne 1956). In the Kayenta Formation skull lengths are: (1) 8–26 cm for *Kayentatherium wellesi* (Kermack 1982; Sues 1986a, 1986b); (2) 2.4 cm for an immature specimen of *Oligokyphus* (Sues 1985); (3) a minimum of 9.5 cm for *Dinnebitodon amarali* on the basis of a partial skull (Sues 1896a); and (4) > 24 cm for an unidentified specimen (Kermack 1982). A *Kayentatherium* with a skull length of ~ 26 cm indicates a body length of ~ 130 cm, consistent with the size of the Type II burrows.

ALTERNATIVE INTERPRETATIONS

Alternative interpretations proposed for Types I and II burrows include rhizoliths, termite nests and other invertebrate trace fossils, fluid-escape features, and wind-erosion features. All of these structures have been identified in association with the Types I and II burrows, and are important for interpreting the paleoecological setting of the Navajo Sandstone in the Moab area. This study demonstrates that the architectural and surficial morphology of Types I and II burrows are distinctly different from these proposed structures.

Rhizoliths.—Rhizoliths are abundant in the study localities (Fig. 3, 17) and have previously been identified in the Navajo Sandstone (Loope 1988; Parrish and Falcon-Lang 2007; Hasiotis and Odier, unpublished data). Rhizoliths have been identified previously based on their two-part structure of a core of sand-free, micritic calcite enveloped by a sheath of calcite-cemented sand (Loope 1988). They are also brown to gray, calcite cemented, and exhibit root-like patterns in outcrop and in thin section that crosscut bedding. Rhizoliths are commonly cylindrical in cross section and bifurcate laterally or downward, decreasing in diameter in third-, fourth-, and fifth-order branches (Fig. 17A, B). They are 3.4–8.58 cm wide 2.8–4.3 cm high (avg. = 5.35 cm wide, 3.15 cm high), and generally smaller and more cylindrical in diameter compared to Type I burrows. The surficial morphology is distinct and composed of rough, almost jagged, surfaces (Fig. 17E). Better-preserved rhizoliths contain alveolar texture, interpreted as closely spaced submillimeter-size rhizoliths (Klappa 1980; Alonso-Zarza et al. 2008). Rhizoliths indicate that roots grew into or along Type I burrows that were previously filled, following a path of least resistance (Fig. 17C). Some rhizoliths can be rather large in size and misinterpreted as burrows if sample sizes are small or preservation is poor.

Figure 17—Rhizoliths in the Navajo Sandstone. A) Branching rhizoliths. B) Small-diameter round rhizolith. C) Rhizoliths on the outer surface of an element. D, E) Rhizoliths extending up out of the Navajo Sandstone. Black or white bar on scale = 1 cm.

Invertebrate Bioturbation.—Type I burrow casts show evidence of reworking by invertebrates (Fig. 18); however, they were not originally excavated as a mass of individual or interconnected small-diameter burrows (Fig. 11B). Burrows 3–5 mm in diameter preserved in positive and negative relief (Fig. 11B, 18B) are most similar to *Planolites*, previously described from the Navajo Sandstone (Ekdale et al. 2007), and are associated with Type I burrows. They

occur in high density below interdune deposits, although in less abundance. Invertebrates that constructed *Planolites* likely lived within, or in the vicinity of, the Type I burrows because their fill was less consolidated, and rhizoliths associated with the burrows may have provided a source of nutrients. Thin-section evidence supports this interpretation (Fig. 18C, D). Other burrows characterized by backfill menisci are 3–7 mm in diameter, unlined, and unbranched, and crosscut one another with no preferred orientation (Fig. 18A). These burrows are best assigned to *Naktodemasis bowni* (Smith et al. 2008), and occur in sediments surrounding the burrows.

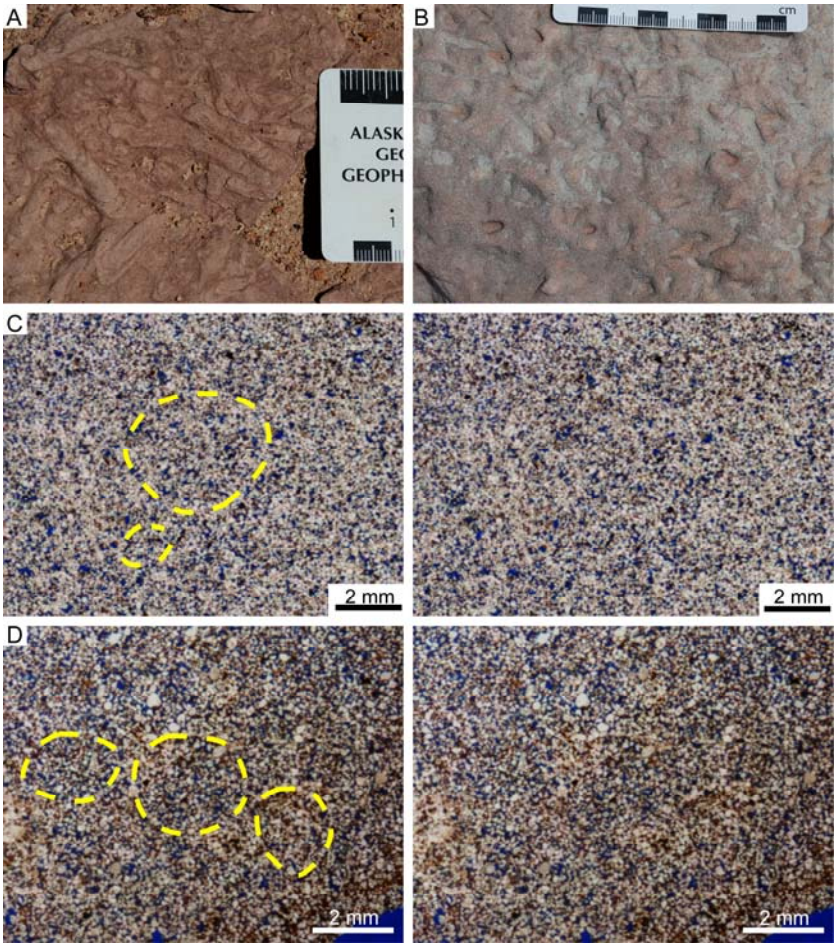

Figure 18—Invertebrate bioturbation in the Navajo Sandstone. A). *Naktodemasis* below an interdune deposit at locality 3. B). *Planolites* beneath interdune deposits at locality 2. C, D). Thin-section evidence of reworking by invertebrates of Type I burrow fill. Red outline shows burrows.

Fluid–Escape Pipes.—Fluid-escape pipes (Fig. 19) are commonly found in the Entrada, Carmel, Page, and Navajo Formations in several locations in south-central Utah (Netoff and Shroba 2001; Netoff 2002; Huuse et al. 2005; Hasiotis et al. 2007b; Hasiotis and Odier, unpublished data). They are formed by the liquefaction of a packed grain framework so that the grains are suspended in a pore fluid followed by resettling into a packed grain framework (Lowe 1975). Fluid-escape pipes within, above, and below the Navajo Sandstone all share similar morphologies: vertical to nearly vertical, generally cylindrical structures—some project out into structureless, tongue-like bodies of sand—that crosscut bedding (Figs. 19A, B, D). The diameters of fluid-escape pipes range from ~ 5 cm to up to 75 m (Nefoff 2002; Hasiotis et al. 2007b; Hasiotis and Odier, unpublished data). Many contain brecciated blocks that vary in size and are similar to the host rock. Concentric layering is commonly visible inside of the fluid-escape pipes (Fig. 19C); however, some pipes are massive (Netoff and Shroba 2001; Netoff 2002; Huuse et al. 2005). None of the morphological features typical of fluid-escape pipes conforms to the morphologies exhibited to Types I and II burrow casts.

Wind-Eroded Features.—Wind-eroded features similar in size and shape to Type I and II burrow casts occur in the Navajo Sandstone (Fig. 20). Wind and water can create rocks with unique architectures (Lancaster 1984). These features, however, are generally simple, singular tubes that rarely branch and do not have helical ramps, bilobate morphology, scratch or scalloped marks, or enlarged terminations. These features are variable in size and appear to gradually change shape and merge with smaller bed sets and weathered outcrop surfaces. The most convincing evidence of these features is primary sedimentary bedding seen on the surface and throughout the structures (Fig. 20A–C), which is vertically continuous from top to bottom and

laterally continuous with the surrounding dune, indicating they are likely wind-eroded and water-worn from overland flow and freeze-thaw activity.

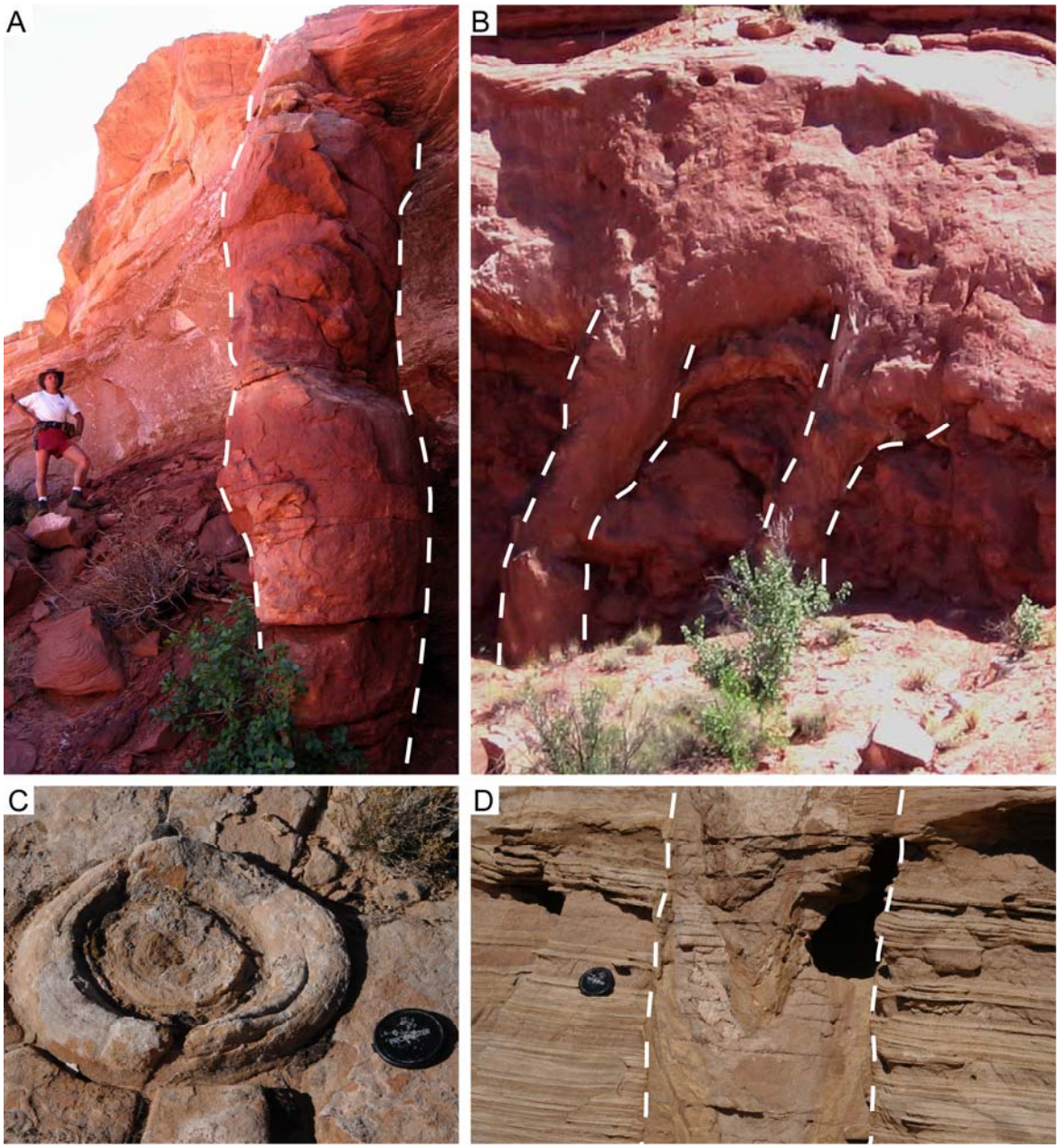

Figure 19—Fluid-escape pipes. A) Large fluid-escape pipe in the Entrada Sandstone. B) Two large fluid-escape pipes in the Entrada Sandstone. C) Small-diameter fluid-escape pipe with concentric rings. Lens cap 6.2 cm. D) Fluid-escape pipe with well defined boundaries.

Figure 20—Eroded rock remnants with morphology similar to that of burrow casts. A) Rock remnant showing laminations on the surface. B) Rock remnant showing lamination on the surface. C) Cross section of Figure 19A showing lamination. Black or white bar on scale = 1 cm.

PALEOECOLOGICAL IMPLICATIONS

The ecology of modern deserts is complex, limited, and controlled by infrequent and unpredictable water input (Noy-Meir 1973; Louw and Seely 1982), and serves as a model to interpret the paleontological evidence from the Navajo Sandstone. Abundant ichnofossils in interdune deposits in association with known body fossils and rhizoliths demonstrates the presence of a viable desert ecosystem in the Early Jurassic (Loope 1988; Winkler et al. 1991; Irmis 2005; Parrish and Falcon-Lang 2007). Wet interdune environments are ideal to sustain habitable environments for organisms because interdune environments would have been stable

geomorphic surfaces with the most productivity in terms of contribution to total biomass of an ecosystem (e.g., Ahlbrandt et al. 1978; Seely and Louw 1980; Louw and Seely 1982).

The presence of tree stumps, logs, rhizoliths, and pollen in the Navajo Sandstone (Gilland 1979; Loope 1988; Parrish and Falcon-Lang 2007) indicates that water was present in the interdune environment as relatively shallow groundwater and localized lakes and springs. The type and distribution of vegetation would have been intimately linked with water availability, and was the primary energy source for other trophic levels (i.e., herbivores, insectivores, carnivores) in the ecosystem. The presence of insects, represented by *Termitichnus* (Hasiotis et al. 2007b), *Planolites*, and *Naktodemasis*, would have been major consumers of vegetative material in the interdune environments, and would also have been the major decomposers that returned nutrients to the desert ecosystem (e.g., Louw and Seely 1982). Tracemakers of *Termitichnus* likely consumed rhizoliths and woody material above and below ground. Tracemakers of *Planolites* and *Naktodemasis* likely consumed the small rhizoliths and organic debris in the sediment. Herbivorous and carnivorous vertebrates represent secondary and tertiary consumers and were fossorial or cursorial in the desert ecosystem.

To survive in extreme environments, organisms developed different morphological, physiological, and behavioral adaptations (e.g., Louw and Seely 1982). The rarity of body fossils in the Navajo Sandstone hinders interpretation of morphological or physiological responses and adaptations of organisms living in desert ecosystems. Ichnofossils, however, are useful for interpreting the behavioral responses of organisms living in desert ecosystems. A major behavioral adaptation was burrowing, represented by Types I and II burrow casts. Burrowing allowed organisms to extend their habitats into normally uninhabitable environments by creating favorable microenvironments with consistent humidity and temperature compared to surface

conditions (Voorhies 1975a; Lynch; 1980; Louw and Seely 1982; Hickman 1990). Microclimates result from such factors as soil, vegetation cover, and burrow depth (e.g., Reichman and Smith 1990; Šumbera et al. 2008). Many extant organisms in a variety of environments construct burrows for thermoregulation (Auffenberg and Weaver 1969; Lynch 1980; Louw and Seely 1982; Reichman and Smith 1990; Kinlaw 1999; Šumbera et al. 2008; Anderson and Richardson 2005). Helical burrows used for thermoregulation have been suggested for late Paleozoic and Mesozoic therapsids (Smith 1987; Meyer 1999; Hasiotis et al. 2004), and the Cenozoic beaver *Paleocastor* (Martin and Bennett 1977; Meyer 1999).

Burrows are often occupied by different species of organisms at the same time or after the original excavator abandoned the burrow (Kinlaw 1999). Evidence for reworking of unconsolidated burrow fills in the Navajo Sandstone by invertebrates and root systems show that these structures were used by several different organisms for refuge, nutrients produced from the excavators within the burrows, or for providing a path of least resistance for digging.

CONCLUSIONS

Enigmatic structures in the Lower Jurassic Navajo Sandstone are interpreted as vertebrate burrows. The burrows either underlie or are within carbonate or mudstone beds that represent deposits of lakes or springs produced from monsoonal rains. There are two major types of burrows based on their architectural and surficial morphologies. The most abundant are Type I burrow casts, which are composed of a complex network of horizontal to subhorizontal, interconnected sinuous tunnels, with Y- and T-branching, helical ramps, and terminal chambers. Burrow walls are predominantly smooth; however, a few exhibit scalloped features. Type I burrows compare well with extant eusocial and social mole-rat and vole burrows, and are most

similar to permanent burrow systems used for foraging, nesting, raising young, and escaping predators. Type I burrows are assigned to polychresichnia, because the architecture represents simultaneous, multiple behaviors and uses. These burrows likely created a microclimate that modulated fluctuations of humidity and temperature compared to the surface, allowing the organism to inhabit the Navajo desert. Although no body fossils of mammals are present, the known occurrence of mammals in the Jurassic Period indicates that these burrows may represent hidden biodiversity in the Navajo Sandstone.

Type II burrow casts are rare and are composed of larger diameters and simple inclined tunnels. One of these burrows has a raised floor with a bilobate morphology similar to that found in Permian and Early Triassic therapsid burrows of South Africa. Type II burrows exhibit well-preserved scratch marks on the lower and upper margin of the burrow, indicating that one large individual, most likely a therapsid, excavated them. The behaviors represented by the Type II burrows are more difficult to discern because only two specimens are partially exposed. Type II burrows are more similar to burrows constructed by alligators, monitor lizards, and armadillos, rather than burrows constructed by mammals.

Opportunity for future research in the Navajo Sandstone abounds, in that much work still needs to be done at many localities in and outside of the Moab area that are unstudied. Types I and II burrows have recently been found but not studied in detail in the Navajo Sandstone south of Moab, (Hasiotis and Rasmussen, unpublished data). Prospecting in interdune deposits preserved as siltstones and mudstones is important because of the likelihood of finding burrows with well-preserved architectural and surficial morphologies such as those of the Type II burrows. Skeletal elements associated with the burrows may eventually be discovered with these and other large-diameter burrows in the Navajo Sandstone. Skeletal elements can be used as

strong evidence for the excavator of the burrows if the claws of the organism can be matched to the scratch marks of the burrows in question. The strongest evidence for the excavator would be finding a skeleton of appropriate size and shape in the shaft, tunnels, or terminal chambers.

ACKNOWLEDGMENTS

We thank A. Rosales for assistance with fieldwork, R. Goldstein for assistance with petrographic analyses, and L. Martin for discussions on fossil vertebrate burrows and Late Triassic and Early Jurassic vertebrates. DJR was funded by the University of Kansas Department of Geology, a Geological Society of America graduate student research grant, and American Association of Petroleum Geologists Grants-in-Aid. The IchnoBioGeoScience (IBGS) research group provided useful comments and suggestions for the manuscript. We thank R. Smith, D. Loope, J. MacEachern, and P. McCarthy for reviews that improved the manuscript.

REFERENCES

AHLBRANDT, T.S., ANDREWS, S., and GWYNNE, D.T., 1978, Bioturbation of eolian deposits: Journal of Sedimentary Petrology, v. 48, p. 839–848.

ALONSO-ZARZA, A.M., GENISE, J.F., CABRERA, M.C., MANGAS, J., MARTIN-PÉREZ, A., VALDEOLMILLOS, A., and DORADO-VALIÑO, M., 2008, Megarhizoliths in Pleistocene aeolian deposits from Gran Canaria (Spain): Ichnological and palaeoenvironmental significance: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 265, p. 39–51.

ANDERSON, M.D., and RICHARDSON, P.R.K., 2005, The physical and thermal characteristics of aardwolf dens: South African Journal of Wildlife Research, v. 35, p. 147–153.

AUFFENBERG, W., and WEAVER, W.G., JR., 1969, *Gopherus berlanceri* in southeastern Texas: Florida State Museum Bulletin, v. 13, p. 141–203.

BEGALL, S., and GALLARDO, M.H., 2000, *Spalacopus cyanus* (Rodentia: Octodontidae): an extremist in tunnel constructing and food storing among subterranean mammals: Journal of Zoology (London), v. 251, p. 53–60.

BAIRD, D., 1980, A prosauropod dinosaur trackway from the Navajo Sandstone (Lower Jurassic), *in* Jacobs, L.L., ed., Aspects of Vertebrate History: Essays in Honor of Edwin Harris Colbert: Museum of Northern Arizona Press, Flagstaff, p. 219–230.

BENTON, M.J., 1988, Burrowing by vertebrates: Nature, v. 331, p. 17–18.

BOWN, T.M., and KRAUS, M.J., 1983, Ichnofossils of the alluvial Willwood Formation (Lower Eocene), Big Horn Basin, northwest Wyoming, U.S.A: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 43, p. 95–128.

BURNS, J.A., FLATH, D.L., and CLARK, T.W., 1989, On the structure and function of white-tailed prairie dog burrows: Great Basin Naturalist, v. 49, p. 517–524.

CARLSON, K.J., 1968, The skull morphology and aestivation burrows of the Permian lungfish, *Gnathorhiza serrata*: Journal of Geology, v. 76, p. 62–71.

CARROLL, R.L., 1965, Lungfish burrows from the Michigan Coal Basin: Science, v. 148, p. 963–964.

CLARK, J.M., MONTELLANO, M. HOPSON, J.A., HERNANDEZ, R., and FASTOVSKY, D.E., 1994, An Early or Middle Jurassic tetrapod assemblage from the La Boca Formation, northeastern Mexico, *in* Fraser, N.C., and Sues, H.-D., eds., In the Shadow of the Dinosaurs: Early Mesozoic Tetrapods: New York, Cambridge University Press, 435 p.

COX, G.W., 1984, The distribution and origin of Mima mound grasslands in San Diego County, California: Ecology, v. 65 p. 1397–1405.

DALQUEST, W.W., and SCHEFFER, V.B., 1942, The origin of the Mima mounds of western Washington: Journal of Geology, v. 50, p. 68–84.

DALQUEST, W.W., and CARPENTER, R.M., 1977, A new discovery of fossil lungfish burrows: Texas Journal of Science, v. 26, p. 611.

DAMIANI, R., MODESTO, S., YATES, A., and NEVELING, A., 2003, Earliest evidence of cynodont burrowing: Royal Society of London, Proceedings, v. 270, p. 1747–1751.

DAVIES, K.C., and JARVIS, J.U.M., 1986, The burrow systems and burrowing dynamics of the mole-rats *Bathygergus hottentotus* in the fynbos of the south-western Cape, South Africa: Journal of Zoology (London), v. 209, p. 125–147.

EISENBERG, L., 2003, Giant stromatolites and a supersurface in the Navajo Sandstone, Capital Reef National Park, Utah: Geology, v. 31, p. 111–114.

EKDALE, A.A., and PICARD, M.D., 1985, Trace fossils in a Jurassic eolianite, Entrada Sandstone, Utah, U.S.A., *in* Curran, H.A., ed., Biogenic Structures: Their Use in Interpreting Depositional Environments: SEPM, Special Publication, v. 35, p. 3–12.

EKDALE, A.A., BROMLEY, R.G., and LOOPE, D.B., 2007, Ichnofacies of an ancient erg: A climatically influenced trace fossil association in the Jurassic Navajo Sandstone, southern Utah, USA: *in* Miller, W., III., ed., Trace Fossils—Concepts, Problems, Prospects: Amsterdam, Elsevier, p. 196–218.

GILLAND, J.K., 1979, Paleoenvironment of a carbonate lens in the Lower Navajo Sandstone near Moab, Utah: Utah Geology, v. 6, p. 29–37.

GOBETZ, K.E., 2005, Claw impressions in the walls of modern mole (*Scalopus aquaticus*) tunnels as a means to identify fossil burrows and interpret digging movements: Ichnos, v. 12, p. 227–231.

GOBETZ, K.E., 2006, Possible burrows of mylagaulids (Rodentia: Aplodontoidea: Mylagaulidae) from the late Miocene (Barstovian) Pawnee Creek Formation, northeastern Colorado: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 237, p. 119–136.

GOBETZ, K.E., and MARTIN, L.D., 2006, Burrows of a gopher-like rodent, possibly *Gregorymys* (Geomyoidea: Geomyidae: Entoptychtinae), from the early Miocene Harrison Formation, Nebraska: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 237, p. 305–314.

GROENEWALD, G.H., WELMAN, J., and MACEACHERN, J.A., 2001, Vertebrate burrow complexes from the early Triassic Cynognathus Zone (Driekoppen Formation, Beaufort Group) of the Karoo Basin, South Africa: Palaios, v. 16 p. 148–160.

HARSHBARGER, J.W., REPENNING, C.A., and IRWIN, J.H., 1957, Stratigraphy of the Uppermost Triassic and the Jurassic Rocks of the Navajo Country: U.S. Geological Survey, Professional Paper 291, 74 p.

HASIOTIS, S.T., 2002, Continental Trace Fossils: SEPM, Short Course Notes, 51, 132 p.

HASIOTIS, S.T., 2003, Complex ichnofossils of solitary to social soil organisms: understanding their evolution and roles in terrestrial paleoecosystems: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 192, p. 259–320.

HASIOTIS, S.T., 2004, Reconnaissance of Upper Jurassic Morrison Formation ichnofossils, Rocky Mountain Region, USA: paleoenvironmental, stratigraphic, and paleoclimatic significance of terrestrial and freshwater ichnocoenoses: Sedimentary Geology, v. 167, p. 177–268.

HASIOTIS, S.T., and BOURKE, M.C., 2006, Continental trace fossils and museum exhibits: displaying burrows as organism behavior frozen in time: The Geological Curator, v. 8, p. 211–226.

HASIOTIS, S.T., MITCHELL, C.E., and DUBIEL, R.F., 1993, Application of morphologic burrow interpretations to discern continental burrow architects: lungfish or crayfish?: Ichnos, v. 2, p. 315–333.

HASIOTIS, S.T., PLATT, B.F., HEMBREE, D.I., and EVERHEART, M.J., 2007a, The trace-fossil record of vertebrates, *in* Miller, W. III., ed., Trace Fossils—Concepts, Problems, Prospects: Amsterdam, Elsevier, p. 196–218.

HASIOTIS, S.T., ODIER, G., RASMUSSEN, D., and MCCORMICK, T., 2007b, Preliminary report on new vertebrate burrow localities in the Lower Jurassic Navajo Sandstone, Moab area, southeastern Utah: architectural and surficial burrow morphologies indicative of mammals or therapsids, and social behavior: (abstract), Geological Society of America, North-Central–South-Central Section Meeting, Lawrence, Kansas, 13 April, v. 39, p. 74.

HASIOTIS, S.T., WELLNER, R.W., MARTIN, A., and DEMKO, T.M., 2004, Vertebrate burrows from Triassic and Jurassic continental deposits of North America and Antarctica: their paleoenvironmental and paleoecological significance: Ichnos, v. 11, p. 103–124.

HEMBREE, D.I., and HASIOTIS, S.T., 2006, The identification and interpretation of reptile ichnofossils in paleosols through modern studies: Journal of Sedimentary Research, v. 76, p. 575–588.

HEMBREE, D.I., and HASIOTIS, S.T., 2008, Miocene vertebrate and invertebrate burrows defining compound paleosols in the Pawnee Creek Formation, Colorado, U.S.A: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 270, p. 349–365.

HEMBREE, D.I., HASIOTIS, S.T., and MARTIN, L.D., 2004, Amphibian burrows and ephemeral ponds of the Lower Permian Speiser Shale, Kansas: evidence for seasonality in the midcontinent: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 203, p. 127–152.

HEMBREE, D.I., MARTIN, L.D., and HASIOTIS, S.T., 2005, *Torridorefugium eskridgensis* (new ichnogenus and ichnospecies): Amphibian aestivation burrows from the Lower Permian Speiser Shale of Kansas: Journal of Paleontology, v. 79, p. 583–593.

HERBST, M., and BENNETT, N.C., 2006, Burrow architecture and burrowing dynamics of the endangered Namaqua dune mole rat (*Bathyergus janetta*) (Rodentia: Bathyergidae): Journal of Zoology, v. 270, p. 420–428.

HICKMAN, C.G., 1990, Adaptiveness of tunnel system features in subterranean mammal burrows, *in* Nevo, E., Reig, O.A., eds., Evolution of Subterranean Mammals at the Organismal and Molecular Levels: New York, Wiley-Liss, p. 185–210.

HILDEBRAND, M., 1974, Analysis of Vertebrate Structure: New York, John Wiley & Sons, 710 p.

HORWATH, J.L., and JOHNSON, D.L., 2006, Mima-type mounds in southwest Missouri: expressions of point-centered and locally thickened biomantles: Geomorphology, v. 77, p. 308–319.

HUNT, R.M., XIANG-XUE, X., and KAUFMAN, J., 1983, Miocene burrows of extinct bear dogs: indication of early denning behavior of large mammalian carnivores: Science, v. 221, p. 354–366.

HUUSE, M., SHOULDERS, S.J., NETOFF, D.I., and CARTWRIGHT, J., 2005, Giant sandstone pipes record basin-scale liquefaction of buried dune sands in the Middle Jurassic of SE Utah: Terra Nova, v. 17, p. 80–85.

IRMIS, R.B., 2005, A review of the vertebrate fauna of the Lower Jurassic Navajo Sandstone in Arizona: Mesa Southwest Museum Bulletin, v. 11, p. 55–71.

JARVIS, J.U.M., and BENNETT, N.C., 1991, Ecology and behavior of the family Bathyergidae, *in* Sherman, P.W., Jarvis, J.U.M., Alexander, R.D., eds., The Biology of the Naked Mole-Rat: Princeton, N.J., Princeton University Press, p. 66–69.

JARVIS, J.U.M., and SALE, J.B., 1971, Burrowing and burrow patterns of east African mole-rats *Tachyoryctes, Heliophobius, Heterocephalus*: Journal of Zoology (London), v. 163, p. 451–479.

JARVIS, J.U.M., O'RAIN, M.J., BENNETT, N.C., and SHERMAN, P.W., 1994, Mammalian eusociality: a family affair: Trends in Ecology and Evolution, v. 9, p. 47–51.

JENKINS, F.A., JR., and PARRINGTON, F.R., 1976, The postcranial skeletons of the Triassic mammals *Eozostrodon*, *Megazostrodon*, and *Erythrotherium*: Royal Society of London, Philosophical Transactions, v. 273, p. 387–431.

JENKINS, F.A., JR., and SCHAFF, C.R., 1988, The Early Cretaceous mammal *Gobiconodon* (Mammalia, Triconodonta) from the Cloverly Formation in Montana: Journal of Vertebrate Paleontology, v. 8, p. 1–24.

JENKINS, F.A., JR., CROMPTON, A.W., and DOWNS, W.R., 1983, Mesozoic mammals from Arizona: new evidence on mammalian evolution: Science, v. 222, p. 1233–1235.

JI, Q., LUO, Z.-X., and JI, S., 1999, A Chinese triconodont mammal and mosaic evolution of the mammalian skeleton: Nature, v. 398, p. 326–330.

KERMACK, D.M., 1982, A new tritylodontid from the Kayenta Formation of Arizona: Zoological Journal of the Linnean Society, v. 76, p. 1–17.

KIELAN-JAWOROWSKA, Z., CIFELLI, R.L., and LUO, Z., 2004, Mammals from the Age of Dinosaurs: Origins, Evolution, and Structure: New York, Columbia University Press, 630 p.

KINLAW, A., 1999, A review of burrowing by semi-fossorial vertebrates in arid environments: Journal of Arid Environments, v. 41, p. 127–145.

KLAPPA, C.F., 1980, Rhizoliths in terrestrial carbonates: classification, recognition, genesis, and significance: Sedimentology v. 26, p. 613–629.

KRAUS, M.J., and HASIOTIS, S.T., 2006, Significance of different modes of rhizoliths preservation to interpreting paleoenvironmental and paleohydrologic settings: Examples from Paleogene paleosols, Bighorn Basin, Wyoming, U.S.A.: Journal of Sedimentary Research, v. 76, p. 633–646.

KOCUREK, G., 2003, Limits on extreme eolian systems: Sahara of Mauritania and Jurassic Navajo Sandstone examples, *in* Chan, M.A., and Archer, A.W., eds., Extreme Depositional Environments: Mega End Members in Geologic Time: Geological Society of America Special Paper 370, p. 43–52.

KÜHNE, W.G., 1956, The Liassic Therapsid *Oligokyphus*: London, Trustees of the British Museum, 149 p.

LANCASTER, N., 1984, Characteristics and occurrence of wind erosion features in the Namib Desert: Earth Surface Processes and Landforms, v. 9, p. 469–478.

LOCKLEY, M.G., 2005, Enigmatic dune walkers from the abyss: some thoughts on water and track preservation in ancient and modern deserts: Canyon Legacy, v. 54, p. 43–51.

LOCKLEY, M., and HUNT, A.P., 1995, Dinosaur Tracks and Other Fossil Footprints of the Western United States: New York, Columbia University Press, 338 p.

LOCKLEY, M., YANG, S.Y., MATSUKAWA, M., FLEMING, F., and LIM, S.K., 1992, The track record of Mesozoic birds: evidence and implications: Royal Society of London, Philosophical Transactions, Biological Sciences, v. 226, p. 113–134.

LOCKLEY, M., HUNT, A.P., MEYER, C., RAINFORTH, E.C., and SCHULTZ, R.J., 1998, A survey of fossil footprint sites at Glen Canyon National Recreation Area (western USA): a case study in documentation of trace fossil resources at a national preserve: Ichnos, v. 5, p. 177–211.

LOOPE, D.B., 1988, Rhizoliths in ancient eolianites: Sedimentary Geology, v. 56, p. 301–314.

LOOPE, D.B., 2006a, Burrows dug by large vertebrates into rain-moistened Middle Jurassic dunes: The Journal of Geology, v. 114, p. 753–762.

LOOPE, D.B., 2006b, Dry-season tracks in dinosaur-triggered grainflows: Palaios, v. 21, p. 132–142.

LOOPE, D.B., 2008, Life beneath the surface of active Jurassic dunes: burrows from the Entrada Sandstone of south-central Utah: Palaios, v. 23, p. 411–419.

LOOPE, D.B., and ROWE, C.M., 2003, Long-lived pluvial episodes during deposition of the Navajo Sandstone: The Journal of Geology, v. 111, p. 223–232.

LOOPE, D.B., ROWE, C.M., and JOECKEL, R.M., 2001, Annual monsoon rains recorded by Jurassic dunes: Nature, v. 412, p. 64–66.

LOOPE, D.B., EISENBERG, L., and WAISS, E., 2004a, Navajo sand sea near-equatorial Pangea: tropical westerlies, slumps, and giant stromatolites, *in* Nelson, E.P., and Erslev, E.A., eds., Field Trips in the Southern Rocky Mountains, USA: Geological Society of America, Field Guide 5, p. 1–13.

LOOPE, D.B., STEINER, M.B., ROWE, C.M., and LANCASTER, N., 2004b, Tropical westerlies over Pangaean sand seas: Sedimentology, v. 51, p. 315–322.

LOVEGROVE, B.G., 1991, Mima-like mounds *(heuweltjies*) of South Africa: the topographical, ecological and economic impact of burrowing animals, *in* Meadows, P.S., and Meadows, A., eds., The Environmental Impact of Burrowing Animals and Animal Burrows: New York, Oxford University Press, p. 183–197.

LOUW, G.N., and SEELY, M.K., 1982, Ecology of Desert Organisms: New York, Longman, 194 p.

LOWE, D.R., 1975, Water escape structures in coarse-grained sediments: Sedimentology, v. 22, p. 157–204.

LUCAS, S.G., and HUNT, A.P., 1990, The oldest mammal: New Mexico Journal of Science, v. 30, p. 41–49.

LUCAS, S.G.., GOBETZ, K.E., ODIER, G.P., MCCORMICK, T., and EGAN, C., 2006, Tetrapod burrows from the Lower Jurassic Navajo Sandstone, Southeastern Utah: New Mexico Museum of Natural History and Science, Bulletin 37, p. 147–154.

LUO, Z.-X., CROMPTON, A.W., and SUN, A.-L., 2001, A new mammaliaform from the Early Jurassic and evolution of mammalian characteristics: Science, v. 292, p. 1535–1540.

LYNCH, C.D., 1980, Ecology of the Suricate, *Suricata suricatta* and Yellow Mongoose, *Cynictis pencillata* with Special Reference to Their Reproduction: Bloemfontein, National Museum Memoirs 14, 145 p.

MANKIN, P.C., and GETZ, L.L., 1994, Burrow morphology as related to social organization of *Microtus ochrogaster*: Journal of Mammalogy, v. 75, p. 492–499.

MARTIN, L.D., and BENNETT, D.K., 1977, The burrows of the Miocene beaver *Palaeocastor*, western Nebraska, U.S.A: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 22, p. 173–193.

MAYES, P.J., 2007, The use of burrows and burrow characteristics of the semi-aquatic *Varanus mertensi* (Reptilia: Varanidae): Mertensiella, v. 16, p. 312–321.

MCKENNA, M.C., and BELL, S.K., 1997, Classification of Mammals Above the Species Level: New York, Columbia University Press, 547 p.

MEYER, R.C., 1999, Helical burrows as a paleoclimate response: *Daimonelix* by *Palaeocastor*: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 147, p. 291–298.

MILLER, M.F., HASIOTIS, S.T., BABOCK, L.E., ISBELL, J.L., and COLLINSON, J.W., 2001, Tetrapod and large burrows of uncertain origin in Triassic high paleolatitude floodplain deposits, Antarctica: Palaios, v. 16, p. 218–232.

NETOFF, D., 2002, Seismogenically induced fluidization of Jurassic erg sands, South-Central Utah: Sedimentology, v. 49 p. 65–80.

NETOFF, D., and SHROBA, R.R., 2001, Conical sandstone landforms cored with clastic pipes in Glen Canyon National Recreation Area, southeastern, Utah: Geomorphology, v. 39, p. 99–110.

NEVO, E., 1999, Mosaic Evolution of Subterranean Mammals: Regression, Progression, and Convergence: New York, Oxford University Press, 413 p.

NOWAK, R.M., 1991, Walker's Mammals of the World: Baltimore, Johns Hopkins University Press, 1629 p.

NOY-MEIR, I., 1973, Desert Ecosystems: environment and producers: Annual Review of Ecology and Systematics, v. 4, p. 25–51.

OLSON, E.C., and BOLLES, K., 1975, Permo-Carboniferous fresh water burrows: Fieldiana Geology, v. 33, p. 271–290.

PARRISH, J.T., and FALCON-LANG, H.J., 2007, Coniferous trees associated with interdune deposits in the Jurassic Navajo Sandstone Formation, Utah, USA: Palaeontology, v. 50, p. 829–843.

RAINFORTH, E.C., and LOCKLEY, M.G., 1996, Tracking life in a Lower Jurassic desert: vertebrate tracks and other traces from the Navajo Sandstone: Museum of Northern Arizona, Bulletin 60, p. 285–289.

REICHMAN, O.J., AND SMITH, S.C., 1990, Burrows and burrowing behavior by mammals, *in* Genoways, H.H., ed., Current Mammalogy: New York, Plenum Press, p. 197–244.

ROMER, A.S., and OLSON, E.C., 1954, Aestivation in a Permian lungfish: Breviora, v. 30, p. 1–8.

SCHMEISSER, R.L., LOOPE, D.B., and WEDIN, D.A., 2009, Clues to the medieval destabilization of the Nebraska Sand Hills, USA, from ancient pocket gopher burrows: Palaios, v. 24, p. 809–817.

SEELY, M.K., and LOUW, G.N., 1980, First approximation of the effects of rainfall on the ecology and energetics of a Namib Desert dune ecosystem: Journal of Arid Environments, v. 3, p. 25–54.

SEILER, W.M., and CHAN, M.A., 2008, A wet interdune dinosaur trampled surface in the Jurassic Navajo Sandstone, Coyote Buttes, Arizona: rare preservation of multiple track types and tail traces: Palaios, v. 23, p. 700–710.

SMITH, C.F., 1948, A burrow of the pocket gopher (*Geomys bursarius*) in eastern Kansas: Kansas Academy of Science, Transactions, v. 51, p. 313–315.

SMITH, R.M.H., 1987, Helical burrow casts of therapsid origin from the Beaufort Group (Permian) of South Africa: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 60, p. 155–170.

SMITH, J.J., HASIOTIS, S.T., KRAUS, M.J., and WOODY, D.T., 2008, *Naktodemasis Bowni*: new ichnogenus and ichnospecies for adhesive meniscate burrows (AMB), and paleoenvironmental implications, Paleogene Willwood Formation, Big Horn Basin, Wyoming: Journal of Paleontology, v. 82, p. 267–278.

SPINKS, A.C., and BENNETT, N.C., JARVIS, J.U.M., 2000, A comparison of the ecology of two populations of the common mole-rat, *Cryptomys hottentotus hottentotus:* the effect of aridity on food, foraging and body mass: Oecologia, v. 125, p. 341–349.

SUES, H.-D., 1984, Inferences concerning feeding and locomotion in the Tritylodontidae (Synapsida), *in* Reif, W.-E., and Westphal, F., eds., Third Symposium on Mesozoic Terrestrial Ecosystems Short Papers: Tübingen, Tübingen University Press, p. 231–236.

SUES, H.-D., 1985, First record of the trityolodontid *Oligokyphus* (Synapsida) from the Lower Jurassic of western North America: Journal of Vertebrate Paleontology, v. 5, p. 328–335.

SUES, H.-D., 1986a, *Dinnebitodon amarali*, a new tritylodontid (Synapsida) from the Lower Jurassic of western North America: Journal of Paleontology, v. 60, p. 758–762.

SUES, H.-D., 1986b, The skull and dentition of two tritylodontids synapsids from the Lower Jurassic of western North America: Museum of Comparative Zoology at Harvard College, Bulletin 151, p. 217–268.

SUES, H.-D., CLARK, J.M., and JENKINS, F.A., JR., 1994, A review of the Early Jurassic tetrapods from the Glen Canyon Group of the American Southwest, *in* Fraser, N.C. and Sues, H.-

D., eds., In the Shadow of the Dinosaurs: Early Mesozoic Tetrapods: New York, Cambridge University Press, p. 284–294.

ŠUMBERA, R., ŠKĽIBA, J., ELICHOVÁ, CHITAUKALI, W.N., and BURDA, H., 2008, Natural history and burrow system architecture of the silvery mole-rat from *Brachystegia* woodland: Journal of Zoology, v. 274, p. 77–84.

TANNER, L.H., SMITH, D.L., and LUCAS, S.G., 2006, Trace fossils in eolian facies of the Upper Triassic-Lower Jurassic Dinosaur Canyon Member, Moenave Formation, Northern Arizona: Ichnos, v. 13, p. 21–29.

VLECK, D., 1981, Burrow structure and foraging costs in the fossorial rodent, *Thomomys bottae*: Oecologia, v. 49, p. 391–396.

VOORHIES, M.R., 1974, Fossil pocket mouse burrows in Nebraska: American Midland Naturalist, v. 91, p. 492–498.

VOORHIES, M.R., 1975a, Vertebrate burrows, *in* Frey, R.W., ed., The Study of Trace Fossils: New York, Spring-Verlag, p. 325–350.

VOORHIES, M.R., 1975b, A new genus and species of fossil kangaroo rat and its burrow: Journal of Mammalogy, v. 56, p. 160–176.

WINKLER, D.A., JACOBS, L.L., CONGLETON, J.D., and DOWNS, W.R., 1991, Life in a sand sea: biota from Jurassic interdunes: Geology, v. 19, p. 889–892.

ZUG, G.R., VITT, L.J, and CALDWELL, J.P., 2001, Herpetology: San Diego, Academic Press, 630 p.

CHAPTER 3. *LABYRINTHOPOLIS ODIERI* AND *SCHEMALITUS PSALIHYPONOMES* (NEW ICHNOGENERA AND ICHNOSPECIES): VERTEBRATE BURROWS IN THE LOWER JURASSIC NAVAJO SANDSTONE, UTAH USA

ABSTRACT

Two types of large-diameter burrows found below interdune lake deposits of the Lower Jurassic Navajo Sandstone near Moab, Utah, are interpreted as vertebrate in origin. Architectural elements of Type I burrows comprise sinuous, Y- and T-branched tunnels and ramps, some which terminate in chambers. Burrows infilled with structureless sand are dorsoventrally flattened in cross section and average 9.3 cm wide and 4.2 cm high. Burrows surfaces predominantly have smooth walls, although some have scalloped surfaces. Type I burrows likely represent permanent dwelling structures for foraging, nesting, hiding, and food storage, and were excavated by fossorial social or eusocial mammals, and are assigned to polychresichnia. Type I burrows represent a new ichnogenera and ichnospecies *Labyrinthopolis odieri*. Type II burrows comprises two dorsoventrally flattened specimens, 35 cm wide and 18 cm high and 58 cm wide and 18 cm high. Burrows are simple, subhorizontal tunnels with sets of three to four, subhorizontal scratches on burrow walls. Type II burrows likely represent a permanent shelter used for dwelling and brooding, and was excavated by a large tritylodontid therapsid based on the large size. Type II burrows represents a new ichnogenera and ichnospecies *Schemalitus psalihyponomes*. *L. odieri* and *S. psalihyponomes* are associated with rhizoliths and invertebrate bioturbation record a viable desert ecosystem in the Navajo Sandstone.

INTRODUCTION

This paper presents two new ichnotaxa of vertebrate burrows, *Labyrinthopolis odieri* n. igen. and n. isp (Type I) and *Schemalitus psalihyponomes* n. igen. and n. isp (Type II) occurring in the Lower Jurassic Navajo Sandstone near Moab, Utah. An objective of this paper is to discuss possible behaviors and excavators represented by *L. odieri* and *S. psalihyponomes*, and their implications to the paleoecology of the Navajo Sandstone. Comparisons of type I–II burrows are made to other large-diameter burrows from continental strata attributed to vertebrate burrowers. Those burrows placed in open nomenclature may be assigned to these new ichnotaxa.

The number of fossil vertebrate burrows discovered has increased recently, and they are recognized in strata as old as the Devonian (Martin and Bennett, 1977; Hunt et al., 1983; Smith, 1987; Groenewald et al., 2001; Miller et al., 2001; Damiani et al., 2003; Hasiotis, 2002; Hasiotis et al., 1999; 2004, 2007a; Hembree et al., 2004, 2005; Gobetz, 2006; Gobetz and Martin, 2006; Loope, 2006a, 2008; Hembree and Hasiotis, 2006, 2008, Lucas et al., 2006). Fossil vertebrate burrows are found in lithologies that represent fluvial floodplain, lacustrine, or palustrine environments (e.g., Smith, 1987; Groenewald et al., 2001; Miller et al., 2001; Hasiotis et al., 2004, 2007a; Hembree and Hasiotis, 2008). Relatively few fossil vertebrate burrows are found in eolian deposits (Voorhies, 1975; Martin and Bennett, 1977; Gobetz and Martin, 2006; Loope, 2006a, 2008).

Most fossil vertebrate burrows described in the literature are placed in open nomenclature. The purpose of ichnotaxonomy is to characterize trace fossils because of their potential utilization in reconstructing paleoenvironmental, paleoecological, and paleoclimatic conditions (Magwood, 1992; Seilacher, 1992; Pickerill, 1994; Bromley, 1996; Bertling et al., 2006). Proper ichnotaxonomic classification of trace fossils is based on such objective criteria as architectural and surficial morphologies (Magwood, 1992; Seilacher, 1992; Pickerill, 1994;

Bromley, 1996). Vertebrates with similar anatomy can produce traces with similar morphologies. Amphibians, reptiles, and mammals have bilaterally symmetrical body plans with anteriorly and posteriorly positioned limbs. Their burrows, therefore, will be morphologically similar, but may differ in shape and complexity, reflecting differences in specific behavior. Ichnotaxonomic studies have shown that media (=substrate), behavior, and paleoenvironmental conditions affect the morphology of trace fossils (e.g., Magwood, 1992; Pickerill, 1994; Bromley, 1996).

METHODS AND TERMINOLOGY

Two types of burrow in the Navajo Sandstone were described at four localities near Moab, Utah. A database was constructed with qualitative and quantitative descriptions of architectural and surficial morphologies (Hasiotis and Mitchell, 1993; Hasiotis et al., 1993) of those burrows (Fig. 21; Appendix 1). The architectural morphology includes the burrow shape (diameter = width and height), length of each segment, type (Y, T) and angle of branching, orientation, three-dimensional area dimensions, and complexity and connectivity of burrow elements. Surficial morphology comprises such features on burrow walls as scratches, ridges, pellets, or knobby texture that can vary in size, shape, and orientation; each feature is produced by a specific burrowing mechanism. Burrow fill comprises the composition, texture, and arrangement of grains in the burrow used to determine the relationship of the burrow to the matrix and if the fill was actively or passively produced.

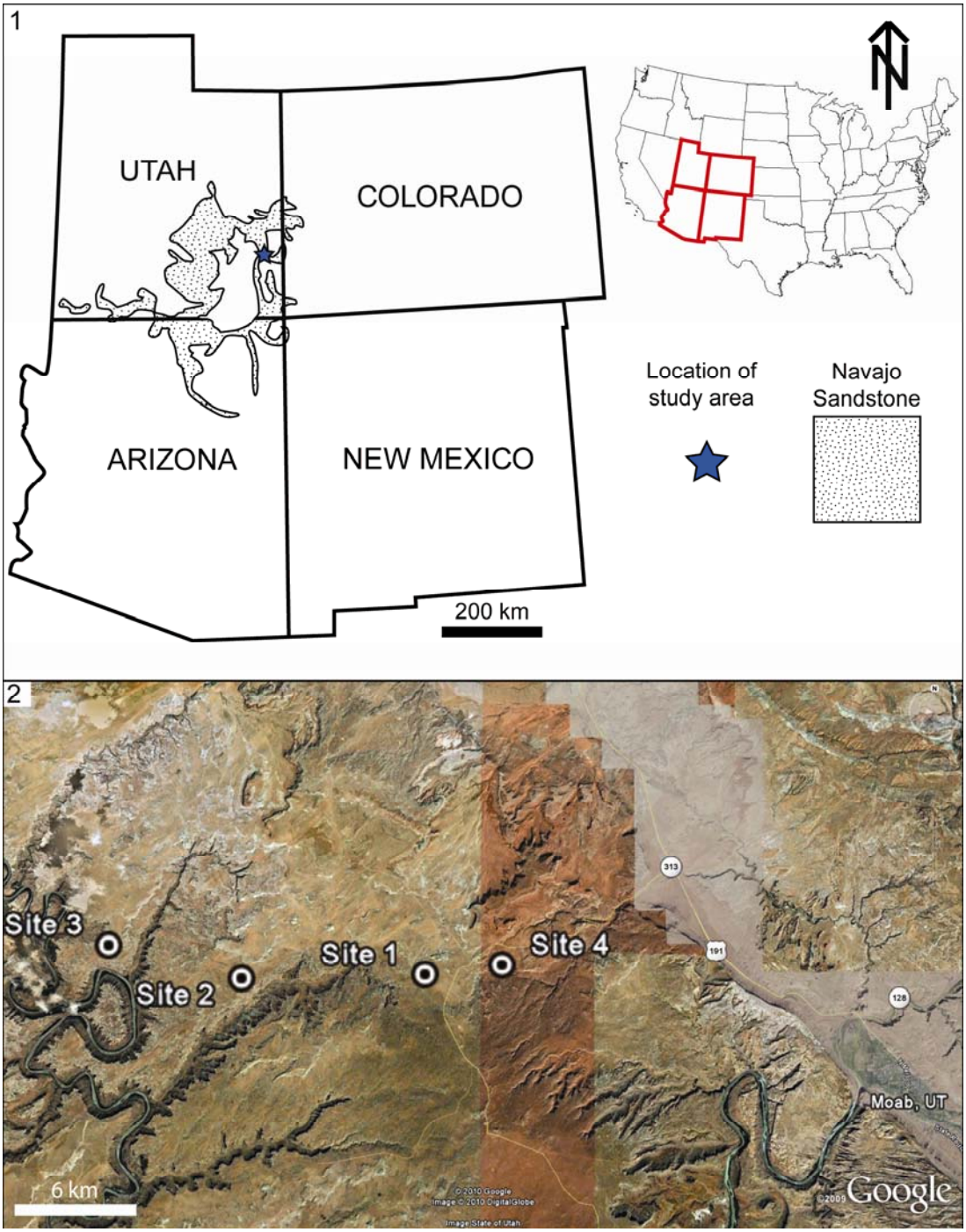

Figure 21—Locality maps. *1,* Map showing location of the Navajo Sandstone that crops out in Utah, Arizona, Colorado, and New Mexico. Star indicates location of study area near Moab, Utah. Modified from Winkler et al. (1991). *2,* Image showing locations of localities investigated near Moab, Utah. Courtesy of Google Earth.

Stratigraphic sections were measured from the base of the Navajo Sandstone and measured a few meters above the highest horizon of burrows (Fig. 22). A section was not measured from the base of the Navajo Sandstone at locality 1, as it is only a surface exposure.

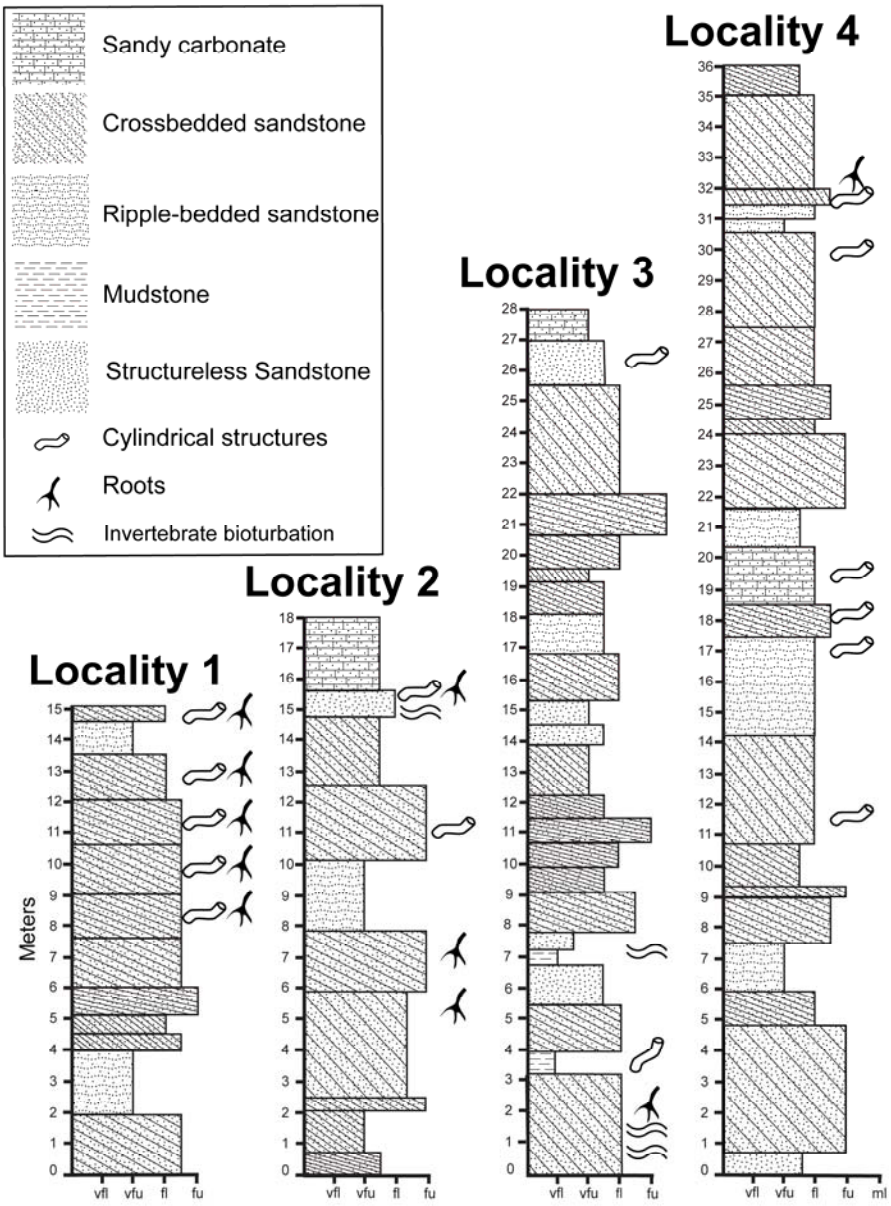

Figure 22—Stratigraphic columns of the four localities investigated.

Type I–II burrows are differentiated based on their architectural and surficial morphologies. Type I burrows are abundant, 4.2–21 cm in diameter, and exhibits complex architecture. Type II burrows are 35–58 cm in diameter and simple in architecture.

Burrow descriptions in the literature may have different terms describing the elements and orientations of burrows that may be interconnected to form a burrow complex or system; therefore, we define the terminology used here (Fig. 23). Tunnel is a horizontal burrow, shaft is a vertical burrow, and ramp is a subhorizontal to subvertical burrow, and helical is a tunnel that curves upward or downward over itself. Chambers are areas have larger diameters relative to tunnels and shafts and can be found in any relationship to elements.

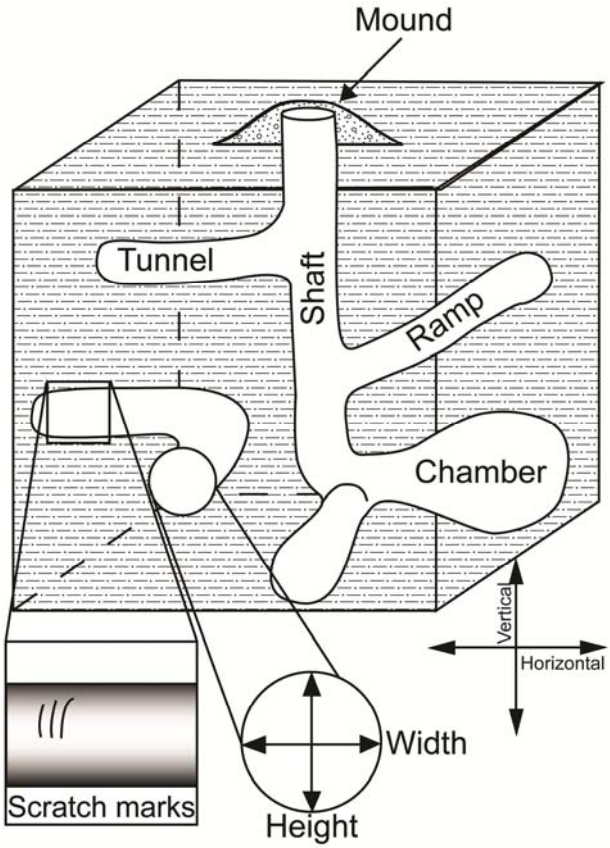

Figure 23—Summary diagram of architectural and surficial morphologies commonly described in vertebrate burrows. Modified from Hasiotis et al. (2007).

GEOLOGICAL BACKGROUND

The Lower Jurassic Navajo Sandstone is part of the Glen Canyon Group and crops out on the Colorado Plateau in southwest U.S.A (Fig. 21) (Harshbarger et al., 1957). The Navajo Sandstone consists of a lower eolian interval, which intertongues with fluvial deposits of the Kayenta Formation, and an upper entirely eolian interval. Large foresets > 20 m thick of very fine- to medium-grained quartzose sandstone (Gilland, 1979) stack vertically throughout the Navajo Sandstone (Kocurek, 2003). Interdune lake deposits include carbonate mounds and flat-lying carbonate beds deposited by nonbiogenic precipitates of spring vents and spring-fed lakes (Gilland, 1979; Parrish and Falcon-Lang, 2007). Interdune deposits also include planar-bedded to structureless mudstone and sandstone (Eisenberg, 2003; Irmis, 2005). Lenticular structureless sandstone beds in interdune deposits are interpreted as mass-flow deposits (Parrish and Falcon-Lang, 2007). Annual summer monsoonal rains recorded by slump deposits in the Navajo Sandstone (Loope et al., 2001, 2004b) produced long-lived pluvial episodes and sustained interdune environments (Winkler et al., 1991; Loope and Rowe, 2003).

Ancient biota preserved in the Navajo Sandstone includes ostracodes, sphenophytes, tritylodontids, theropod dinosaurs, crocodylomorphs, and prosauropods (Winkler et al., 1991; Irmis, 2005; Parrish and Falcon-Lang, 2007). Ichnotaxa recognized in the Navajo Sandstone likely produced from arthropods include *Planolites beverleyensis*, *Palaeophycus tubularis*, *Skolithos linearis*, *Arenicolites* isp., *Taenidium serpentinus*, *Naktodemasis bowni*, and *Termitichnus* isp. (e.g., Loope and Rowe, 2003; Loope et al., 2004a; Ekdale et al., 2007; Riese et al., in press). Rhizoliths, large silicified coniferous tree trunks, and stumps represent plant life (Loope, 1988; Hasiotis et al., 2007b; Parrish and Falcon-Lang, 2007). The few vertebrate trace fossils described from the Navajo Sandstone include dinosaur and reptile tracks, and vertebrate

burrows (Baird, 1980; Lockley et al., 1992, 1998; Lockley and Hunt, 1995; Rainforth and Lockley, 1996; Loope and Rowe, 2003; Irmis, 2005; Lockley, 2005; Loope, 2006b; Lucas et al., 2006; Seiler and Chan, 2008).

Locality Descriptions

Type I–II burrows were investigated at four localities ~32–57 km northwest of Moab, Utah, in the vicinity of Canyonlands National Park (Fig. 21, 22). Type I burrows at locality 1, ~32 km northwest of Moab, are present in mounded areas separated by cross-bedded sandstone. Type I burrows at locality 2, ~48 km northwest from Moab, comprises along a ridge from a stratigraphic horizon ~15 m above the base of the Navajo Sandstone. *Planolites* isp. and *Naktodemasis* isp. are found in deposits that underlie interdune deposits at this locality. Locality 3, ~57 km northwest from Moab, has a Type I burrow-bearing horizon ~26 m above the base of the Navajo Sandstone. Type II burrows occur in a mudstone ~3.5 m above the base of the Navajo Sandstone. A sandy carbonate bed is present above the type I burrows, ~27 m above the base of the Navajo Sandstone. Locality 4, located ~30 km northwest from Moab, comprises three sites. Type I burrows weather out along a ridge ~30 m above the base of the Navajo Sandstone. A few type I burrows occur at ~12 m, and 17–20 m above the base. Rhizoliths are dominant at this locality, and are associated with only type I burrows.

Type I–II burrows are found within several stratigraphic levels of the Navajo Sandstone (Fig. 23). Type I burrow-bearing horizons commonly lack visible bedding. The host rock in which the structures are found is composed of very fine- to fine-grained, buff colored cross-bedded sandstone. In some areas ripple cross-laminated sandstones was present as well. Rhizoliths and invertebrate trace fossils are found in association with the Type I–II burrows at all the localities.

SYSTEMATIC ICHNOLOGY

Ichnogenus LABYRINTHOPOLIS new ichnogenus

Type Ichnospecies.—*LABYRINTHOPOLIS ODIERI* new ichnospecies

Diagnosis.—High density, highly interconnected horizontal to subhorizontal, sinuous, Y- and T-branched, dorsoventrally flattened, unlined burrows.

Etymology.—From Greek, *labyrinthos*, structure with many winding passages, and *polis*, city.

LABYRINTHOPOLIS ODIERI new ichnospecies

Figures 4.1–4.6, 5.2–5.3

Diagnosis.—Only known ichnospecies; same as for genotype.

Description.—*Labyrinthopolis odieri* occurs both as float and more commonly in place as full relief casts. *L. odieri* are infilled with fine-grained sand with no internal structure or lining. *L. odieri* exhibits complex architecture of high-density, interconnected elements with Y- and T-branching, sinuous tunnels, ramps, and chambers elliptical in cross section, and found in mound-like areas, or in areas pervasive over the entire outcrop (Fig. 26). At one locality mounds are clearly distinguishable and range in dimension from 40 m by 40 m to 10 m by 15 m and are ~1 m in height. Orientations of *L. odieri* are horizontal to subhorizontal with ramps measuring 6–60º (average = 24º), from horizontal. *L. odieri* have predominantly flat bottoms, a rounded top, and are flattened dorsoventrally. Dimensions of *L. odieri* ranged from 4.23 to 21 cm wide and 1.16 to 10.22 cm high (average = 9.3 cm wide and 4.2 cm high) (Fig. 27). Interconnected tunnels form Y and T branches with wider dimensions than the tunnels themselves, and comprised angles of branching from 40 to 160º (average = 97º).

Surficial morphology includes scalloped grooves paired on the sides of *L. odieri* interpreted as produced by the animal's claw pushing sediment out on the walls of the burrow. Widths measured from trough to trough of scallops range from 5 to 7 cm (average = 6.4 cm); the scallops protrude outward 0.5–1.5 cm (average = 1 cm) from the surface. Other biogenic structures preserved on the walls and within the burrows include rhizoliths and invertebrate burrows. Rhizoliths are commonly smaller in diameter, and are composed of carbonate gray or darker brown in color with respect to the buff colored *L. odieri*. Invertebrate burrows are preserved with negative and positive relief, randomly oriented cylinders on the burrow walls.

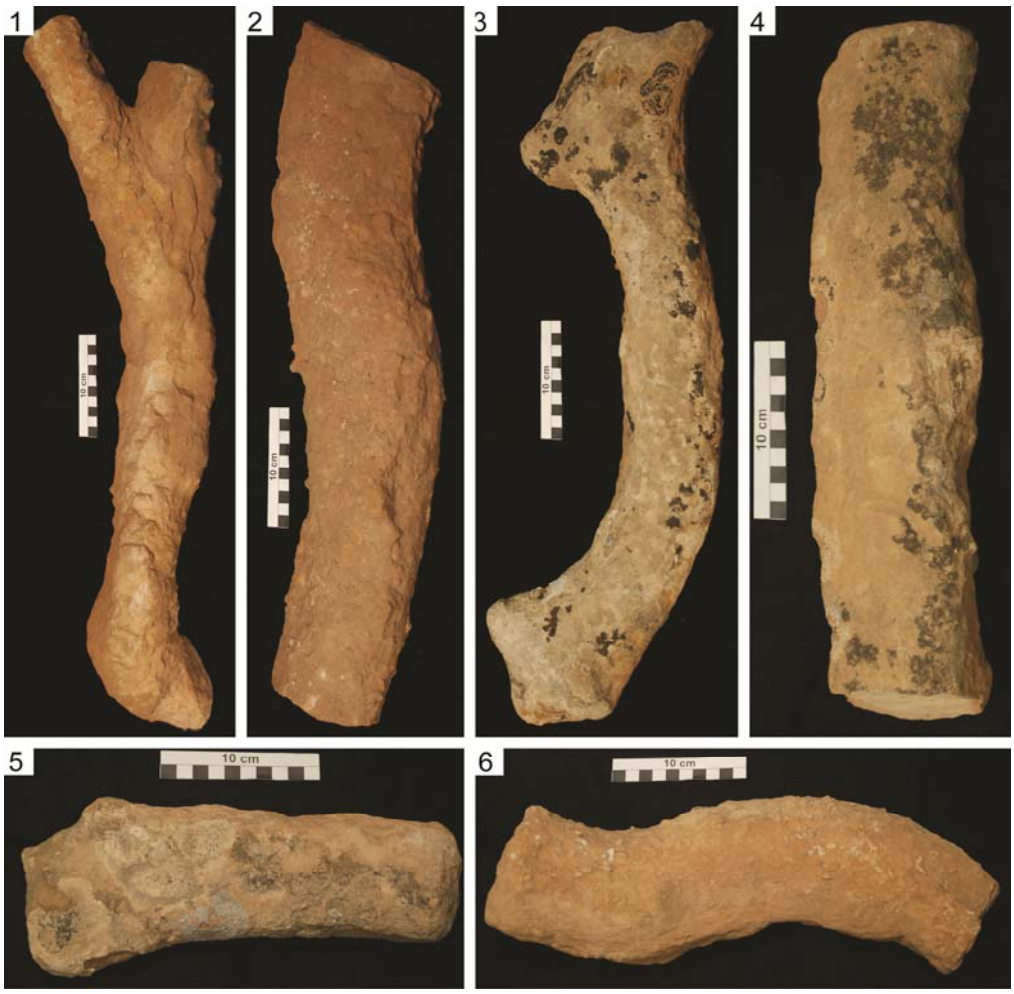

Figure 24—Photographs of *Labyrinthopolis odieri* n. igen. and n. isp. *1, L. odieri* with Y-branching (KUVP 150601). *2, L. odieri* with weak sinuous morphology (KUVP 150597). *3, L. odieri* with a curved morphology (KUVP 150598). *4–5,* Straight segment of *L. odieri* (KUVP 150599–150600). *6, L. odieri* with sinuous morphology (Holotype specimen KUVP 150596). Scales are all 10 cm.

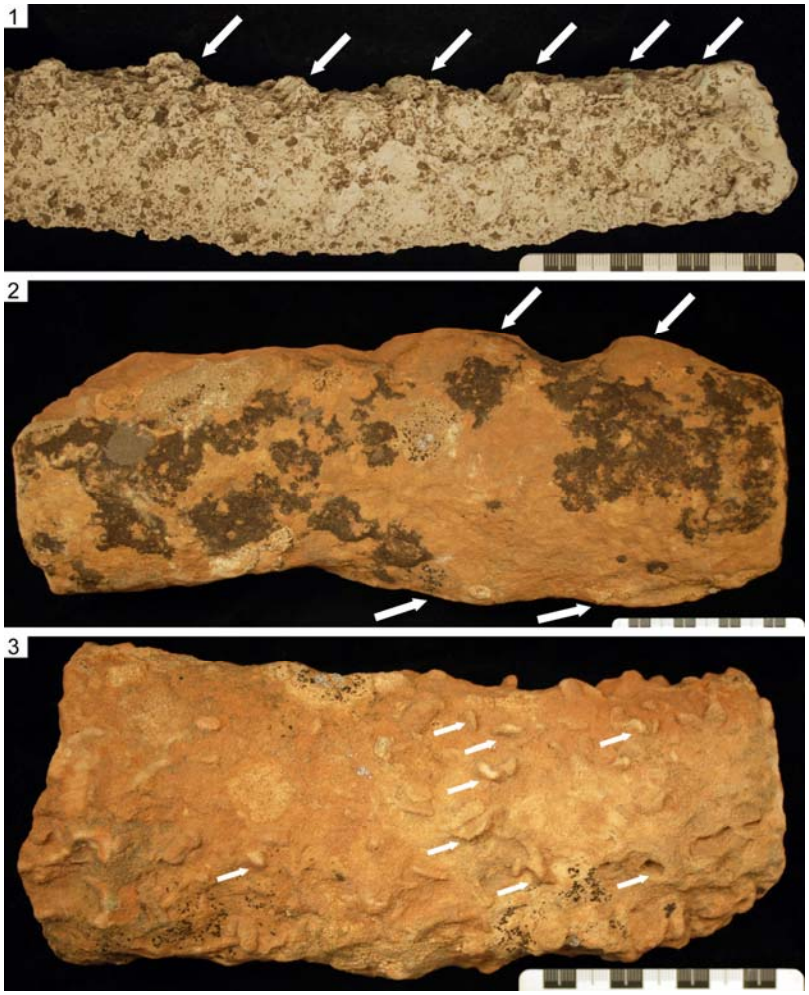

Figure 25—Surficial morphology of *Labyrinthopolis odieri* n. igen. and n. isp. *1,* Plaster cast of a mole burrow with scallop marks produced from the claw pushing on the surface of the burrow. Scallops pointed out by white arrows. *2,* Scallop marks on *L odieri* pointed out by arrows constructed by organism pushing along the walls with their claws. Also notice most specimens of *L. odieri* have a smooth surface (KUVP 150602). *3,* Invertebrate bioturbation observed as small cylindrical projections on *L. odieri* (KUVP 150603). One black or white bar on scale = 1 cm.

Etymology.—Named after Georges Odier who was the first to find and document many of the burrow sites, and how brought these to our attention.

Types.—Holotype, KUVP 150596, paratypes KUVP 150597–150616

Occurrence.—Lower Jurassic Navajo Sandstone, Latitude 38°37′26.82″N Longitude 109°49′38.34″W, Latitude 38°37'19.38"N Longitude 109°55'55.02"W; Latitude 38°38'12.00"N Longitude 110° 0'30.90"W; Latitude 38°37'42.48"N Longitude 109°47'0.42"W.

Figure 26—Architectural morphology of *Labyrinthopolis odieri* n. igen. and n. isp. *1*, Site 1 locality that shows *L. odieri* occurring in high density mounded areas. Person for scale is ~ 5′6″. *2–3*, Close up of mounded areas showing different architectural elements of *L. odieri* displaying multiple branching. *4*,Branching morphology of *L. odieri*. *5*, Sinuous morphology of *L. odieri*. One black or white bar on scale = 1 cm.

Possible behaviors and tracemakers

L. odieri likely represent the work of multiple individuals most similar to social to

eusocial mammals based on the overall size and complexity of the burrow systems. *L. odieri* are likely permanent dwellings used for a variety of behaviors, including foraging, nesting, hiding, and food storage. Complex architectures are exhibited in modern burrow systems that contain one or multiple individuals in a social or eusocial system, and that are also found in areas with limited food supply (Jarvis and Sale, 1971; Davies and Jarvis, 1986; Burns et al., 1989; Reichman and Smith, 1990; Hickman, 1990; Kinlaw, 1999; Nevo, 1999; Herbst and Bennett, 2006). Complex burrows also aid in escape from predators through the use of multiple entrances and exits and bolt-holes—tunnels used to enter a burrow when pursued (Jarvis and Sale, 1971; Benton, 1988; Kinlaw, 1999). *L. odieri*, therefore, are assigned to the behavioral category polychresichnia as the architecture likely represents simultaneous, multiple behaviors and uses (Hasiotis, 2003).

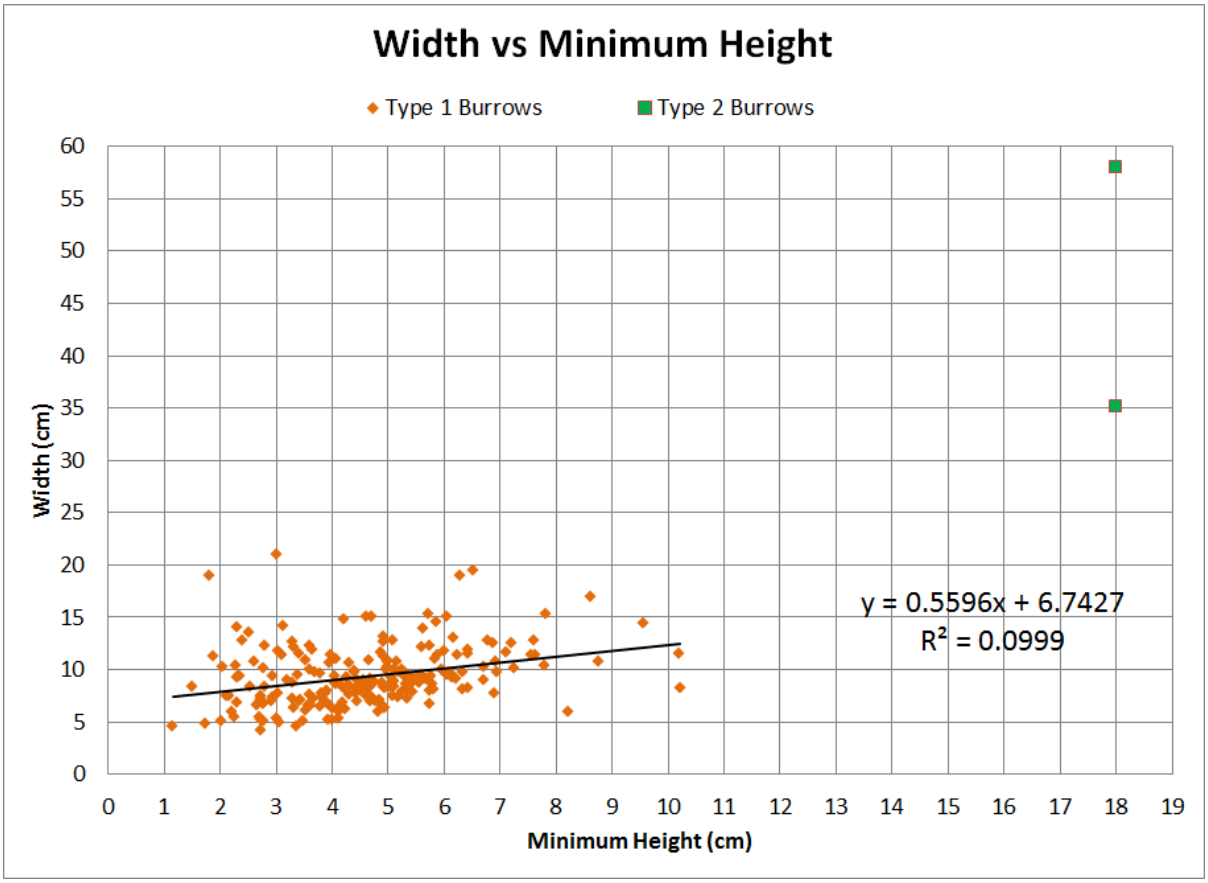

Figure 27—Scatter plot of width to height of *Labyrinthopolis odieri* n. igen. and n. isp. and *Schemalitus psalihyponomes* n. igen. and n. isp.

Although no mammal body fossils have been found in the Navajo Sandstone, at least 8 (e.g., McKenna and Bell, 1997) to 13 (e.g., Kielan-Jaworowska et al., 2004) mammal lineages (order or family level) are present by the Late Jurassic—depending on the classification scheme used. Several possible lineages and one taxon not clearly mammalian are also recognized in North America deposits (Jenkins et al., 1983; Lucas and Hunt, 1990; Kielan-Jaworowska et al., 2004).

Four major mammal lineages existed by the Early Jurassic (Kielan-Jaworowska et al., 2004). Members of the morganucodonta are found in the Lower Jurassic Kayenta Formation in Gold Springs, northern Arizona, and comprise the taxa *Dinnetherium nezorum* and

Morganucodon sp., along with a possible haramiyid represented by a single molariform tooth (Jenkins et al., 1983; Kielan-Jaworowska et al., 2004). Morganucodontans are also found in the La Boca Formation in Huizichal Canyon, Mexico, which comprises a taxon similar to *Dinnetherium* (Clark et al., 1994). Postcranial fossils of morganucodontans are limited, but suggest that these mammals were the size of a shrew to a rat (skull length = 2.7–3.8 cm), and capable of climbing on uneven media (Jenkins and Parrington, 1976; Luo, 2001; Kielan-Jaworowska et al., 2004).

Several skeletal elements are also found in the La Boca Formation, including a triconodont molar similar to molars of two taxa of the eutriconodonta. Eurticonodontans are known from the Middle Jurassic to the Early Cretaceous, with a possible specimen from the Lower Jurassic of India (Kielan-Jaworowska et al., 2004). Eutriconodontans are some of the largest mammals during the Mesozoic (Kielan-Jaworowska et al., 2004) ranging in body size from ~4.4 cm long (*Jeholdens jenkinsi*; Late Jurassic insectivores) to 36 cm long (*Gobicondodon ostromi*; Early Cretaceous carnivore) with a skull length of 2.2–10 cm, respectively. Body size estimation did not include the tail and was based on reconstruction from Ji et al. (1999) and Jenkins and Schaff (1988). These mammals are interpreted as ground-dwellers capable of climbing on uneven media (Ji et al., 1999); the Early Cretaceous example is comparable in body size to the North American Opossum, but with a more robust skeleton. The skeleton was a size comparable to *L. odieri* comes from a morganucodontan with a skull length reaching ~3.8 cm and a possible body length of ~25 cm, comparable to the size of a rat.

Comparison with other ancient vertebrate burrows

Multiple fossil burrow systems have been described that show complex architectures of sinuous, Y- and T- branched tunnels and ramps. Several fossil vertebrate burrows left in open

nomenclature may be placed into *Labyrinthopolis*, and possibly assigned a new ichnospecies owing to differences in the burrow complexity.

Groenewald et al. (2001).—Burrows in the Lower Triassic of South Africa are interpreted to have been excavated by therapsids based on the presence of the therapsid *Trirachodon* in the terminal chambers (Groenewald et al., 2001). These burrows represent the earliest evidence of communal burrowing by tetrapods. The interpretation of a communal burrow was based on the complex architecture, including multiple branching tunnels, a floor with little surficial morphology suggesting constant travel, and the presence of multiple skeletons found in terminal chambers.

Trirachodon burrows are 5–12 cm diameter burrows, elliptical in cross section, with a complex system of tunnels that curve, branch, and converge. Burrow complexity increases with increased depth from the entrance tunnel, which has a large diameter relative to the rest of the burrow and has a bilobate floor with a curved ceiling. Tunnels are inclined 1–23° and become smaller and more flattened distally from the entrance tunnel; the overall shape of the burrow, however, remains the same. Tunnels are predominantly flat at distal portions of the burrow system, but also show a central depression on the ceiling. The terminal chamber is strongly flattened with a central depression and tapers to a rounded edge. The burrows floor, walls, and ceilings commonly preserve a series of scratch marks.

Miller et al. (2001) and Hasiotis (2004).—Burrows in the Lower Triassic Fremouw Formation of Antarctica are interpreted as tetrapod in origin and characterized by elliptical cross sections with 8 to 19 cm diameters with an average of 12.6 cm. The burrows are subhorizontal to gently inclined, and straight to slightly curved with penetration depths typically of 8–25 cm with a maximum of 50 cm. Branching is rare and no lining or mudchips were found on the burrow

margins. Scratch marks are found on the burrow walls oriented tangentially and longitudinally to the axis.

Damiani et al. (2003).—The oldest evidence of burrowing of a cynodont synapsid comes from the Permian-Triassic boundary within the Balfour Formation in the Beaufort Group of the Karoo Basin of South Africa. The specimens found represent the terminal chamber of a burrow. This burrow cast was identified as therapsid in origin by the presence of an articulated skeleton of *Thirnaxodon liorhinus* curled up in the terminal chamber.

T. liorhinus burrows are found as float and have a rounded distal edge. The edge of the terminal chamber appears as though there was a clear break from a tunnel that lead to the terminal chamber. This tunnel was mostly round in cross section, ~15 cm wide and 13 cm high, and with a low bilobate floor and a curved ceiling. A series of scratch marks were found on the sides and lower margins of the ceiling. This partial burrow cast matches the architectural and surficial morphologies of the *Trirachodon* burrows described by Groenwald et al. (2001).

Hasiotis et al. (2004).—Burrows within the Owl Rock Member of the Upper Triassic Chinle Formation are interpreted to have been excavated by mammal-like reptiles. Although the burrow system comprises architectural morphologies that are very similar to extant fossorial mammals, Hasiotis et al. (2004) noted that the mammals in the Late Triassic were not diverse and too small to have constructed the burrows. The Owl Rock Member burrows are described as short, interconnected horizontal tunnels, shafts, spiral shafts and chambers that formed a complex network. The burrow cross sections are generally circular and the dimensions range from 4–15 cm. The surficial morphology of the burrows comprises knobby surfaces and scratch marks produced from either construction or maintenance of the burrow.

Hasiotis et al. (2004).—Burrows from the upper part of the Salt Wash Member of the Upper Jurassic Morrison Formation are interpreted as being excavated by fossorial mammals. The burrow systems comprise short and inclined shafts that form U- or Y-shaped branching patterns. The architectural morphologies of the Salt Wash Member burrows comprise multiple entrance holes connected to shallow or steeply dipping tunnels leading to simple-to-complex interconnected tunnels, shafts, spiral shafts, and chambers of various sizes. The diameters of the tunnels are generally circular, from 5 to 20 cm in diameter, with variable tunnel lengths, some extending over 400 cm. The surficial morphologies of the burrows comprise knobby texture and short to elongate scratch marks.

Hembree and Hasiotis 2008.—Burrows from the Miocene Pawnee Creek Formation of northeastern Colorado assigned to *Polychoredrites tetracheilichnus* are interpreted to be excavated by rodents. *P. tetracheilichnus* comprises a complex system of interconnected subhorizontal to subvertical tunnels. The main tunnel leads to a widened terminal chamber, and side branches also lead to smaller chambers. Inclinations of tunnels range from 10 to 20°. The burrows are elliptical in cross section, ranging from 12 to 15 cm wide and 5 to 8 cm high. The tunnel systems extend laterally 1.5–1.7 m with a depth of 1.1 m. The burrow walls show a multiple series of 3 to 4 parallel scratch marks.

P. tetracheilichnus is similar in architecture to *L. odieri*, but major differences do exist. *L. odieri* comprises more densely packed interconnected tunnels that have a greater lateral extent. Burrow systems of *L. odieri* do contain terminal chambers, but not in the quantity that is seen in the burrow systems of *P. tetracheilichnus*. The surficial morphology of *L. odieri* also does not show scratch marks preserved on the walls of the burrows, but instead several specimens show

scallop marks produced from the organism's claws pushing sediment out on the walls of the burrow.

Gobetz 2006.—Burrows from the Miocene Pawnee Creek Formation of northeastern Colorado assigned to *Alezichnos chelecharatos* are interpreted to be excavated by rodents. *A. chelecharatos* comprises nearly horizontal primary tunnels from which secondary tunnels and shafts arise. The shorter shafts can be inclined 20–60 ° from horizontal and have a sinuous and irregular branching morphology described as a rambling labyrinthine system. Some burrow shafts overlap one another at angles as great as 50°. The burrows are slightly ovate in cross section with diameters from 11.9 to 22 cm wide (average = 16.7 cm) and 9.4 to 20.2 cm high (average = 13.6 cm), and have a length of up to 7 m. Burrow sidewalls and floors, as well as the ceiling of termini, show several sets of two or three scratch marks.

Gobetz and Martin 2006.—Burrows from the early Miocene Harrison Formation in Nebraska assigned to *Alezichnos trogodont* are interpreted to be excavated by gopher-like rodents. The overall architectural morphology is similar to the genus *Alezichnos* with the tubular and sinuous morphology with complex and irregular branching patterns of tunnels. Some of the shafts were weakly helical in morphology. The average diameter of the tunnels ranged from 5.6 to 6.7 cm, but the tunnels tended to change slightly from wider dorsoventrally to wider transversely. The burrow walls show evidence of incisor marks that appear as groove-like, flat-edged marks that sometimes form chevrons. The chambers show evidence of mostly claw marks that appear as ridges regularly spaced apart and sometimes occur on small knob-like projections.

Alezichnos chelecharatos and *Alezichnos trogodont* show very distinct morphologies that distinguish them from *L. odieri*. The most significant difference between these burrows is that *L. odieri* is more elliptical in cross section, and the burrows occur as more densely packed complex

burrow systems that have a greater lateral extent. The complexity of the burrows is also greater because of increase branching and interconnection of architectural elements in close proximity. The surficial morphology of *L. odieri* is also different because there is no evidence of either scratch marks or incisor marks.

Ichnogenus SCHEMALITUS new ichnogenus

Type Ichnospecies.—*SCHEMALITUS PSALIHYPONOMES* new ichnospecies

Diagnosis.—Horizontal to subhorizontal, long, unlined burrow, dorsoventrally flattened, and simple in architecture.

Etymology.—From Greek, *schema*, shape, form, plan, and *litos,* simple.

SCHEMALITUS PSALIHYPONOMES new ichnospecies

Figure 8.1–8.6

Diagnosis.—Only known ichnospecies; same as for genotype.

Description.—*Schemalitus psalihyponomes* is a dorsoventrally flattened tunnel; two specimens have dimensions of 35 cm wide, 18 cm high, and 58 cm wide, 18 cm high (Fig. 28). The best-preserved example of *S. psalihyponomes* is ~6.17 m long and extends from the sandstone into the underlying mudstone at ~25°. The portion of *S. psalihyponomes* in sandstone is poorly preserved for ~4 m as a weathered ledge with mud rip-up clasts delineating the base of the tunnel. The portion of *S. psalihyponomes* in mudstone is well preserved for ~2.2 m and curves into the mudstone until it extends into the outcrop out of view. *S. psalihyponomes* exhibits a bilobate morphology in the mudstone created from a raised floor. The raised floor is 20–25 cm wide, measured from the center of each lobe, and 2–2.5 cm deep, measured from the base of the lobe to

the high crest of the raised floor. The lobe width is ~15–20 cm for both sides exposed in the mudstone. The second structure of *S. psalihyponomes* is seen in cross-section in the mudstone. This structure has massive fill with mudstone clasts on the perimeter of the structure.

Surficial morphology of *S. psalihyponomes* include sets of two or three scratch marks preserved as linear ridges extending from the upper part of the wall and along the lobes of the structure (Fig. 28.5–28.6). Scratch marks range from 4.0 to 8.0 mm wide (average 5 mm) and 2.5 to 20 cm long (average 8.8 cm); distances between individual marks range from 1.5 to 3 cm (average 2.3 cm). Scratch marks from the upper part of the wall of *S. psalihyponomes* are inclined at angles ranging from 14 to 30° (average 23.2°). Scratch marks on the base of the lobe range from 6 to 11 mm wide (average 9 mm) and 3 to 18.5 cm long (average 9.8 cm); distances between individual marks range from 1.3 to 3.5 cm (average 2.6 cm). Scratch marks converge towards the midline at <10°, however, one scratch mark crosscuts others at a 30° angle.

Etymology.—From Greek, *psalis,* low building with a vaulted ceiling, and *hyponomes*, underground passage, tunnel.

Types.—Holotype, KUVP150594 (Fig. 24.1–24.3), paratypes KUVP 150595

Occurrence.—Lower Jurassic Navajo Sandstone, Latitude 38°38'12.00"N Longitude 110° 0'30.90"W

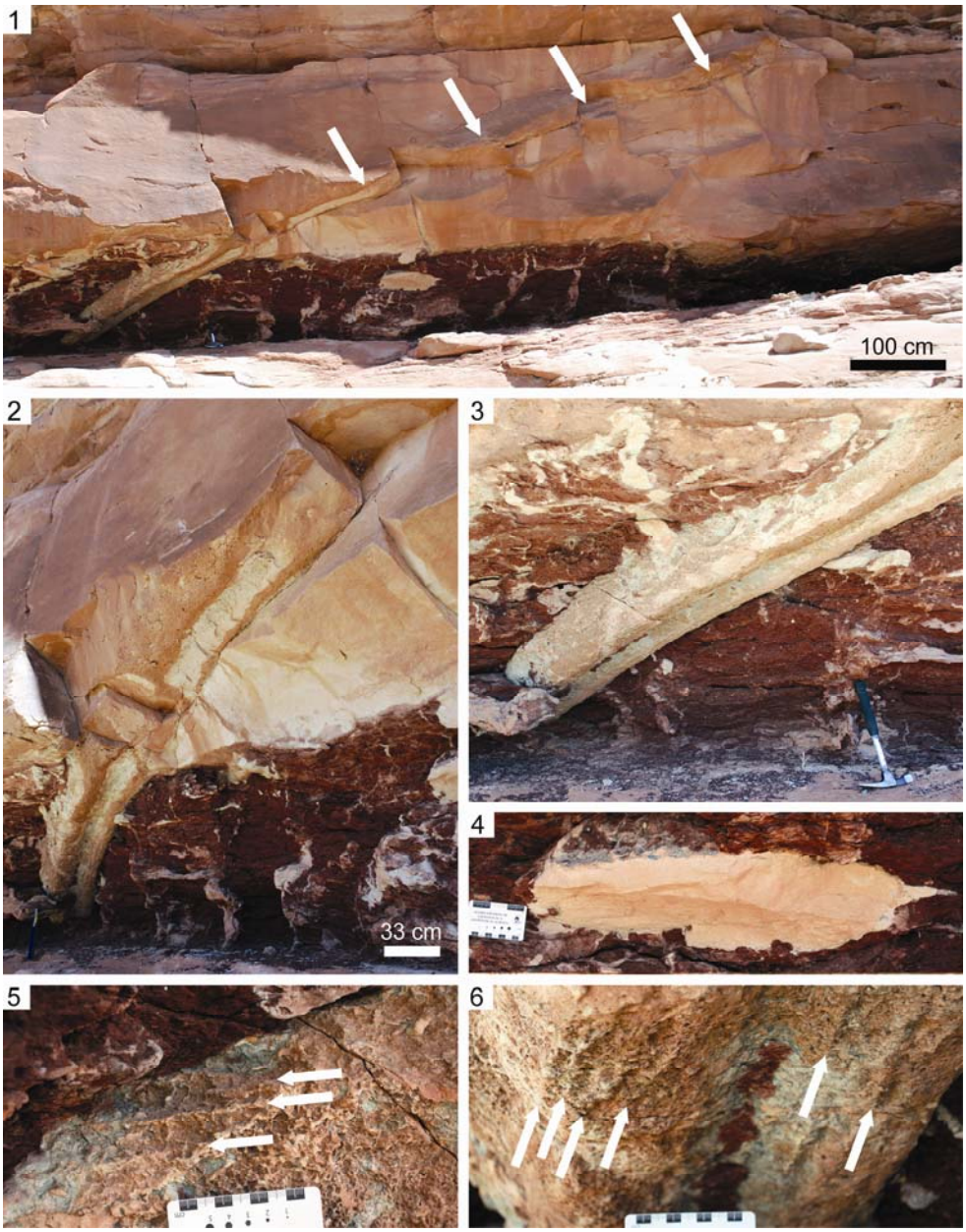

Figure 28—Architectural and surficial morphologies of *Schemalitus psalihyponomes* n. igen. and n. isp. *1*, *S. psalihyponomes* seen extending from the sandstone where it is poorly preserved, into a mudstone where it is well preserved. Person for scale is ~ 5′6″ (KUVP 150594). *2–3,* Well preserved *S. psalihyponomes* seen in mudstone with a raised floor creating a bilobate morphology (KUVP 150594). *4,* Cross sectional view of *S. psalihyponomes* that has a massive fill (KUVP 150595). *5–6,* Scratch marks pointed out by white arrows on the upper sides and bottom of lobes on *S. psalihyponomes* (KUVP 150594).

Possible behaviors and tracemakers

The burrow length and bilobate morphology suggests that the organism would have actively continued to use this burrow and may have tried to seek the more stable interdune mud to produce its terminal chamber. *S. psalihyponomes* likely represent a permanent structure used for dwelling and brooding (i.e., reproduction). Present-day examples of organisms that exhibit analogous behaviors include adult alligators, crocodiles, monitor lizards, and such mammals as the platypus, armadillo, and aardwolf. These organisms spend part of their time in burrows, normally for protection, and often construct simple, sometimes linear tunnels that may have an enlarged chamber at the end (Voorhies, 1975; Reichman and Smith, 1990; Hasiotis et al., 2004; Anderson and Richardson, 2005).

S. psalihyponomes were likely excavated by a large tritylodontid therapsid. A skeleton of a tritylodontid therapsid was found in the Navajo Sandstone in northern Arizona within interdune deposits (Winkler et al., 1991). Winkler et al. (1991) assigned this specimen, interpreted to have a sprawling stance, to *Kayentharium.* Sues et al. (1994), however, found no diagnostic material in the specimen and referred it to Tritylodontidae indet. Sues (1984) hypothesized that tritylodontids were scratch diggers based on such skeletal features as the large olecranon process, which resembles such extant scratch digging mammals as the Mediterranean mole rat (Hildebrand 1974; Winkler et al., 1991).

Several tritylodontid specimens have been found in a sequence of intercalated claystone, sandstone, and siltstone deposits of the Kayenta Formation in northern Arizona (Kermack, 1982; Sues, 1985, 1986a, 1986b). Many of these specimens are incomplete and the studies focus on the dentition rather than postcranial material and, therefore, skull lengths are given for a size reference. As an example of how skull length may relate to total body size, the taxon of *Oligokyphus major* has a skull length of ~9 cm and a body size of ~50 cm including the tail

(Kühne, 1956). In the Kayenta Formation skull lengths are: 1) 8– 26 cm long for *Kayentatherium wellesi* (Kermack, 1982; Sues, 1986a, 1986b); 2) 2.4 cm long for an immature specimen of *Oligokyphus* (Sues, 1985); 3) a minimum of 9.5 cm long for *Dinnebitodon amarali* based on a partial skull (Sues, 1896a); and 4) > 24 cm long for an unidentified specimen (Kermack, 1982). A *Kayentatherium* skeleton with a larger skull length of ~26 cm indicates a total body length of ~130 cm, consistent with the size of *S. psalihyponomes*.

Comparison with other ancient vertebrate burrows

Multiple vertebrate burrows have been described in the fossil record that have simple architectures to *S. psalihyponomes*. Extant organisms that are solitary typically construct simple burrows, or they occupy burrows only for times of protection or brooding (Voorhies, 1975; Reichman and Smith, 1990; Hasiotis et al., 2004; Anderson and Richardson, 2005; Mayes, 2007). Several of these vertebrate burrows are also placed in open nomenclature and, therefore, can be assigned to *Schemalitus* but placed in a new ichnospecies owing to the appearance of branching tunnels or terminal chambers.

Hasiotis et al. (2004).—Burrows in the Upper Jurassic Morrison Formation are interpreted to have been excavated by reptiles similar to crocodiles, alligators, and sphenodontids (Hasiotis et al., 2004). The burrows are subhorizontal tunnels (5–25°) that have a large dimension ranging from 15 to 50 cm (width to height ratio = 1.5–3.5) and are 75 cm to more than 200 cm long. Burrow terminations are often difficult to see, however, they are slightly wider than the diameter of the tunnel. The burrows also show short and long scratch marks.

Loope (2006a).—Burrows found in the eolian cross strata of the upper half of the Escalante Member of the Entrada Sandstone in southern Utah are interpreted to have been excavated by large vertebrates (Loope, 2006a). These burrows were likely produced by animals

digging into rain-moistened, cohesive sand and may have served as temporary shelters from the extreme temperatures. Burrows occur in clusters at second- and third-order bounding surfaces that are inclined from 16–22° from surface of origin. Burrows are typically cylindrical with diameters from 28 to 63 cm wide (average = 41 cm) and maximum lengths from 51 to 305 cm (average = 141 cm). A few of the burrows ended in enlarged chambers ~63 cm in diameter. Three different materials infill the burrows: cross strata, breccias, and structureless sand. Cross strata were interpreted as sand drifts migrating into the abandoned burrow, whereas breccias and structureless sand were generated by roof collapse.

Hembree and Hasiotis 2008.—Burrows from the Miocene Pawnee Creek Formation of northeastern Colorado assigned to *Katarrhedrites athesphatichnus* are interpreted to be excavated by a large mammal carnivore. The burrow is described as a large subhorizontal tunnel inclined 15–20° from the paleosurface that flattens to 1–5° at the base of the burrow. The tunnel opening was poorly defined, but the diameter of the burrow is 60–70 cm at the entrance and widens to 80–85 cm at the terminal chamber. The total length of the burrow is 1.85 m and penetrates to a depth of 1.0–1.1 m. No surficial morphology was seen on the burrow surfaces.

K. athesphatichnus shows major differences compared to *S. psalihyponomes*. The most significant difference is *S. psalihyponomes* is much longer then *K. athesphatichnus*; the *Schemalitus* specimen are not even completely exposed. *K. athesphatichnus* also shows a terminal chamber, however, because *S. psalihyponomes* is not completely exposed, a terminal chamber may be found in future studies. The other major difference is *S. psalihyponomes* is elliptical in cross section, has a raised floor creating a bilobate morphology, and also preserves a series of scratch marks.

Sidor et al. (2008).—Burrows found in the Middle Triassic Lashly Formation in Antarctica are interpreted to have been excavated by tetrapods and assigned to open nomenclature. The burrows have been found in the same stratigraphic level as procolophonid skulls, of which juvenile specimens may have been large enough to excavate the burrows, although, it is very speculative. The burrows are simple in architecture, horizontal to gently inclined, and comprise a rounded upper surface and a ventral surface with two lobes separated by a midline trough that creates a bilobate morphology. The burrows are oval in cross section and range from 4.32 to 6.75 cm wide and 2.46 to 3.94 cm high. The total lengths of burrows range from 7.36 to 43.5 cm. Scratch marks are longitudinal on the ventral surface and angled 20° to the horizontal on lateral surfaces of the burrows. These burrows have some similarities with *S. psalihyponomes*, however, *S. psalihyponomes* at ~6 m long, is much longer then the burrows in the Lashly Formation, which are no longer than 43.5 cm.

PALEOECOLOGICAL IMPLICATIONS

Ichnofossils found within and below interdune deposits associated with various body fossils, rhizoliths, tree stumps, logs, and pollen demonstrates the presence of a viable desert ecosystem. The most important and limiting factor to the desert ecosystem was water, which was present as relatively shallow groundwater as well as in localized lakes and springs (Loope, 1988; Winkler et al., 1991; Irmis, 2005; Parrish and Falcon-Lang, 2007). Wet interdune environments are an ideal place to sustain habitable environments for organisms because interdunes are the second most productive in vegetation, and the most stable in terms of contribution to total biomass of an ecosystem after rainstorms compared to dune slope and slipface subenvironments (e.g., Ahlbrandt et al., 1978; Seely and Louw, 1980; Louw and Seely, 1982).

To survive in desert ecosystems, organisms often develop different anatomical, physiological, and behavioral adaptations to tolerate the extreme conditions of arid environments (Louw and Seely, 1982). *L. odieri* and *S. psalihyponomes* are interpreted to represent behavioral adaptations of animals in an arid environment. The burrows represent a refuge that allowed the tracemaker to extend their habitats into normally uninhabitable environments by creating microenvironments in subterranean settings that are more favorable with more consistent humidity, moisture, and temperatures compared to surface conditions (e.g., Voorhies, 1975; Lynch; 1980; Louw and Seely, 1982; Hickman, 1990). The microclimate within burrows can vary based on a variety of such factors as burrow depth, soil type, and vegetative cover (e.g., Reichman and Smith, 1990; Sumbera et al., 2004). Burrows with high humidity often have few surface openings, are often plugged with sediment, or may have complex architectures to limit air circulation (Martin and Bennett, 1977; Reichman and Smith, 1990; Meyer, 1999). Although it is difficult to determine the number of surface openings of *L. odieri*, and whether the surface openings were plugged, the complexity of the burrows may have helped control air circulation to increase humidity.

Many secondary biota likely took advantage of the presence of *L. odieri* and *S. psalihyponomes* in the eolian environment for reasons such as 1). refuge; 2) reproduction; and 3). consumption of food stuffs or organic waste produced by the original excavators or other organisms (e.g. Newman, 1987; Lips, 1991; Anderson and Richardson 2005). Insects were likely attracted to the presence of roots within or along the surfaces of *L. odieri* for food consumption after abandonment and infilling as evidenced by the presence of invertebrate bioturbation throughout *L. odieri* (e.g. Ahlbrandt et al., 1978). Burrows in modern-day desert environments

are often occupied by many different species of organisms either at the same time or after the original excavator abandoned the burrow (Kinlaw, 1999).

Roots within and along the surface of *L. odieri* were present because *L. odieri* provided a path of least resistance as well as an area to obtain water. Roots penetrate soils partly by growing within existing voids, especially in soils with great sediment strength that increases the sediment's resistance to root growth (Taylor, 1971). Favorable conditions of root penetration would have existed within voids found both within an open burrow, and after the burrow was abandoned and infilled between the burrow surface and the host rock. When *L. odieri* was occupied, moisture inside the burrow, created partly by respiration of the organism, likely attracted roots taking advantage of the moisture on the burrow surfaces (e.g. Martin and Bennett, 1977). Water also likely infiltrated along the burrow surfaces after the burrow was abandoned and infilled with sand because of a higher hydraulic conductivity in the voids compared to the host rock attracting the root to grow along this surface. The burrowing activities of animals would have also increased diversity and abundance of plants through alteration of the media, replenishing of nutrients, and increasing water infiltration (e.g., Louw and Seely, 1982; Kalisz and Davis, 1992; Laundre, 1993).

CONCLUSIONS

The new ichnogenera and ichnospecies *Labyrinthopolis odieri* and *Schemalitus psalihyponomes* described from interdune lake deposits of the Navajo Sandstone represent evidence of vertebrates burrowing in an arid environment. *L. odieri* consists of a labyrinth of complex architecture of high-density, interconnected burrow elements, composed of straight to sinuous tunnels that form Y- and T- branches, ramps, and chambers in mound-like areas or in

areas that are pervasive over the entire outcrop (Fig. 29). *L. odieri* represents a permanent dwelling structure likely excavated by fossorial social to eusocial mammals that used the burrow for predator avoidance, foraging, storage of food, reproduction, and nesting. *L. odieri* is assigned to polychresichnia because the architecture represents simultaneous, multiple behaviors and uses (Hasiotis, 2003). The mammal that likely excavated *L. odieri* belongs to the morganucodonta. The new ichnogenera *Labyrinthopolis* may be best applied to the *Trirachodon* burrows described by Groenewald et al. (2001), and may be assigned a different ichnospecies because of the less complex burrow architecture.

S. psalihyponomes is a simple subhorizontal tunnel found in interdune mudstone. The best preserved tunnel has a bilobate morphology created by a raised floor along the burrow axis, and walls with scratch marks on the upper side margin and floor of the burrow (Fig. 28). *S. psalihyponomes* represents a permanent dwelling structure likely excavated by *Kayentatherium*. This organism was an active hunter or scavenger likely during periods of cooler temperatures associated with sunset until sunrise, and escaped to the burrow for refuge during extreme temperatures associated with summer daily temperatures or winter nightly temperatures (e.g., Seely and Louw, 1980; Louw and Seely, 1982). The new ichnogenera and ichnospecies *Schemalitus psalihyponomes* are best assigned to burrows interpreted to have been constructed by reptiles in the Upper Jurassic Morrison Formation (Hasiotis et al., 2004).

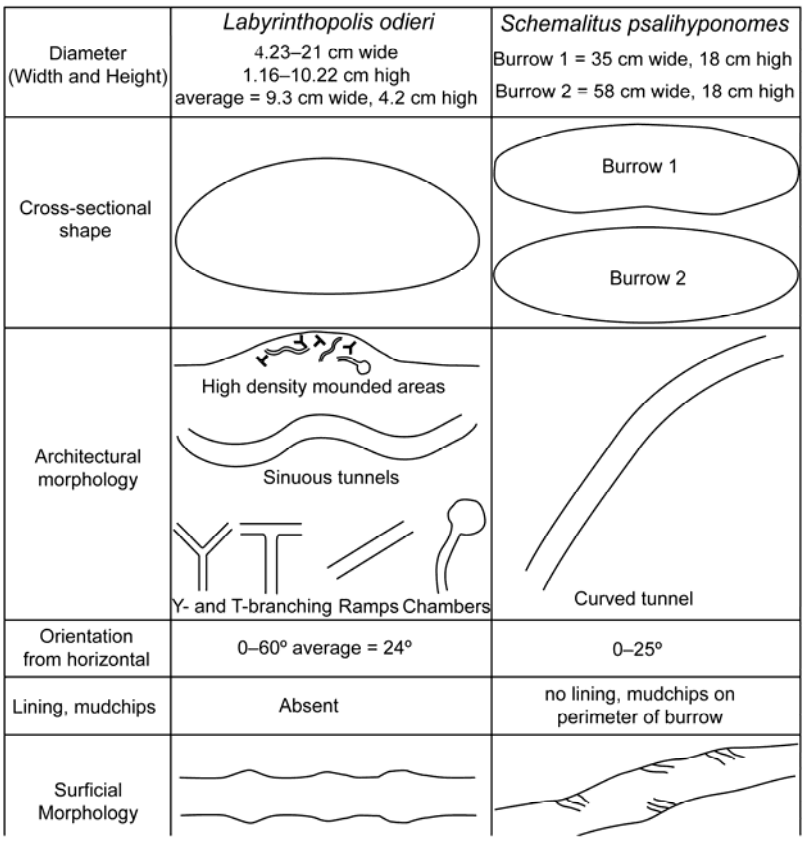

Figure 29—Summary diagram of morphologies seen in *Labyrinthopolis odieri* n. igen. and n. isp. and *Schemalitus psalihyponomes* n. igen. and n. isp.

The association of type I–II burrows, along with rhizoliths, body fossils, and other invertebrate burrows (e.g., Loope, 1988; Winkler et al., 1991; Irmis, 2005; Ekdale et al., 2007; Parrish and Falcon-Lang, 2007; Hasiotis and Odier, unpublished data) demonstrates that wet interdune environments sustained life in this desert ecosystem. Type I–II burrows also show evidence of organisms developing behavioral adaptations to survive in harsh environments of Navajo desert ecosystems for shelter, and type I burrow may also be used for food foraging. Other organisms in the Navajo desert ecosystem likely made use of the burrows excavated for either their own protection in abandoned burrows, or for nutrients buried in infilled burrows.

The number of vertebrate burrows discovered recently in the rock record is on the rise, yet many are placed in open nomenclature. Vertebrate burrows in the Triassic of South Africa, Antarctica, the Chinle Formation, and the Jurassic Morrison Formation are best assigned to the new ichnogenus *Labyrinthopolis* but should be assigned to a new ichnospecies, as they are less complex compared to the type ichnospecies. Vertebrate burrows excavated in the Morrison Formation, and vertebrate burrows in the Entrada Sandstone are best assigned to the ichnogenus *Schemalitus*. The Entrada Sandstone burrows could be assigned a different ichnospecies as they are slightly more circular in diameter and have an enlarged chamber at the terminus of the tunnel.

ACKNOWLEDGMENTS

We are indebted to our friend and colleague Georges Odier who found the burrow localities in the Navajo Sandstone and introduced us to them for study. His passing in August 2009 was unexpected and untimely; may his memory be eternal. We thank A. Rosales for assistance with fieldwork, R. Goldstein for assistance with petrographic analyses, and L. Martin for discussions on fossil vertebrate burrows and knowledge of Late Triassic and Early Jurassic vertebrate fauna. We also thank Paul Selden and Jill Hardesty for reviewing the ichnotaxonomic names. DJR was funded by the University of Kansas Department of Geology, Geological Society of America Graduate Student Research Grant, and American Association of Petroleum Geologists Grants-in-Aid. We thank the 2010 IchnoBioGeoScience research group for comments and suggestions that improved the manuscript. We appreciate the comments and suggestions from xxx and xxx that improved this manuscript.

REFERENCES

AHLBRANDT, T.S., ANDREWS, S. and GWYNNE, D.T., 1978, Bioturbation of eolian deposits: Journal of Sedimentary Petrology, v. 48 p. 839–848.

ANDERSON, M.D., and RICHARDSON, P.R.K., 2005, The physical and thermal characteristics of aardwolf dens: South African Journal of Wildlife Research, v. 35, p. 147–153.

BAIRD, D, 1980, A prosauropod dinosaur trackway from the Navajo Sandstone (Lower Jurassic), *in* Jacobs, L.L. (ed.), Aspects of Vertebrate History: Essays in honor of Edwin Harris Colbert: Museum of Northern Arizona Press, Flagstaff, p. 219–230.

BERTLING, M., BRADDY, S.J., BROMLEY, R.G., DEMATHIEU, G.R., GENISE, J., MIKULÁŠ, R., NIELSEN, J.K., NIELSEN, K.S.S., RINDSBERG, A.K., SCHLIRF, M., and UCHMAN, A, 2006, Names for trace fossils: a uniform approach: Lethaia, v. 39, p. 265–286.

BROMLEY, R.G.,1996, Trace Fossils: Biology and Taphonomy: Chapman and Hall, London, 361 p.

BURNS, J.A., FLATH, D.L., and CLARK, T.W.,1989, On the structure and function of white-tailed prairie dog burrows: Great Basin Naturalist, v. 49, p. 517-524.

DAMIANI, R., MODESTO, S., YATES, A., and NEVELING, J., 2003, Earliest evidence of cynodont burrowing: Proceedings of the Royal Society of London, v. 270, p. 1747–1751.

DAVIES, K.C., and JARVIS, J.U.M., 1986, The burrow systems and burrowing dynamics of the mole–rats *Bathygergus hottentotus* in the fynbos of the south–western Cape, South Africa: The Zoological Society of London, v. 209, p. 125–147.

EISENBERG, L, 2003, Giant stromatolites and a supersurface in the Navajo Sandstone, Capital Reef National Park, Utah: Geology, v. 31, p. 111-114.

GILLAND, J.K, 1979, Paleoenvironment of a carbonate lens in the Lower Navajo Sandstone near Moab, Utah: Utah Geology, v. 6, p. 29–37.

GOBETZ, K.E., 2006, Possible burrows of mylagaulids (Rodentia: Aplodontoidea: Mylagaulidae) from the late Miocene (Barstovian) Pawnee Creek Formation, northeastern Colorado: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 237, p. 119–136.

GOBETZ, K.E., and MARTIN, L.D., 2006, Burrows of a gopher-like rodent, possibly Gregorymys (Geomyoidea: Geomyidae: Entoptychtinae), from the early Miocene Harrison Formation, Nebraska: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 237, p. 305–314.

GROENEWALD, G.H., WELMAN, J., AND MACEACHERN, J.A., 2001, Vertebrate burrow complexes from the early Triassic Cynognathus Zone (Driekoppen Formation, Beaufort Group) of the Karoo Basin, South Africa: Palaios, v. 16, p. 148–160.

HARSHBARGER, J.W., REPENNING, C.A., and IRWIN, J.H., 1957, Stratigraphy of the uppermost Triassic and the Jurassic rocks of the Navajo Country: U.S. Geological Survey Professional Paper, v. 291, 74 p.

HASIOTIS, S.T., 2002, Continental trace fossils: SEPM Short Course Notes, v. 51, p. 1–132.

HASIOTIS, S.T., 2003, Complex ichnofossils of solitary to social soil organisms: understanding their evolution and roles in terrestrial paleoecosystems: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 192, p. 259-320.

HASIOTIS, S.T., 2004, Reconnaissance of Upper Jurassic Morrison Formation ichnofossils, Rocky Mountain Region, USA: paleoenvironmental, stratigraphic, and paleoclimatic significance of terrestrial and freshwater ichnocoenoses: Sedimentary Geology, v. 167, p. 177–268.

HASIOTIS, S.T., MITCHELL, C.E., and DUBIEL, R.F., 1993, Application of morphologic burrow interpretations to discern continental burrow architects: lungfish or crayfish?: Ichnos, v. 2, p. 315–333.

HASTIOTIS, S.T., PLATT, B.F., HEMBREE, D.I., AND EVERHEART, M.J., 2007a, The trace-fossil record of vertebrates, *in* Miller III, W. (ed.), Trace Fossils—Concepts, Problems, Prospects: Elsevier Press, Amsterdam, p. 196–218.

HASIOTIS, S.T., ODIER, G., RASMUSSEN, D., and MCCORMICK, T., 2007b, Preliminary report on new vertebrate burrow localities in the Lower Jurassic Navajo Sandstone, Moab area, southeastern Utah: architectural and surficial burrow morphologies indicative of mammals or therapsids, and social behavior. Abstracts North-central–South-central Geological Society of America Section Meeting, Lawrence, Kansas, 13 April, 1.

HASIOTIS, S.T., WELLNER, R.W., MARTIN, A., and DEMKO, T.M., 2004, Vertebrate burrows from Triassic and Jurassic continental deposits of North America and Antarctica: their paleoenvironmental and paleoecological significance: Ichnos, p. 11, v. 103–124.

HEMBREE, D.I., HASIOTIS, S.T., 2006, The identification and interpretation of reptile ichnofossils in paleosols through modern studies: Journal of Sedimentary Research, v. 76, p. 575–588.

HEMBREE, D.I., HASIOTIS, S.T., 2008, Miocene Vertebrate and Invertebrate Burrows Defining Compound Paleosols in the Pawnee Creek Formation, Colorado, U.S.A: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 270, p. 349–365.

HEMBREE, D.I., HASIOTIS, S.T., and MARTIN, L.D., 2005, *Torridorefugium eskridgensis* (new ichnogenus and ichnospecies): Amphibian aestivation burrows from the Lower Permian Speiser Shale of Kansas: Journal of Paleontology, v. 79, p. 583–593.

HERBST, M., AND BENNETT, N.C., 2006, Burrow architecture and burrowing dynamics of the endangered Namaqua dune mole rat (*Bathyergus janetta*) (Rodentia: Bathyergidae): Journal of Zoology, v. 270, p. 420–428.

HICKMAN, C.G., 1990, Adaptiveness of tunnel system features in subterranean mammal burrows, *in* Nevo E., Reig O.A. (eds.), Evolution of Subterranean Mammals at the Organismal and Molecular Levels: Wiley-Liss, New York, p. 185–210.

HUNT, R.M., XIANG-XU, X., and KAUFMAN, J., 1983, Miocene burrows of extinct bear dogs: indication of early denning behavior of large mammalian carnivores: Science, v. 221, p. 354–366.

IRMIS, R.B., 2005, A review of the vertebrate fauna of the Lower Jurassic Navajo Sandstone in Arizona: Mesa Southwest Museum Bulletin, v. 11, p. 55–71.

JARVIS, J.U.M., and SALE, J.B., 1971, Burrowing and burrow patterns of east African mole–rats *Tachyoryctes, Heliophobius, Heterocephalus*: Journal of Zoology London, v. 163, p. 451–479.

JENKINS, F.A., JR., and PARRINGTON, F.R., 1976, The postcranial skeletons of the Triassic mammals *Eozostrodon*, *Megazostrodon*, and *Erythrotherium*: Philosophical Transactions of the Royal Society of London, v. 273, p. 387–431.

JENKINS, F.A., JR., and SCHAFF, 1988, The Early Cretaceous mammal *Gobiconodon* (Mammalia, Triconodonta) from the Cloverly Formation in Montana: Journal of Vertebrate Paleontology, v. 8, p. 1–24.

JENKINS, F.A., JR., CROMPTON, A.W., and DOWNS, W.R., 1983, Mesozoic mammals from Arizona: new evidence on mammalian evolution: Science, v. 222, p. 1233–1235.

JI. Q., LUO, Z., and JI.,S., 1999, A Chinese triconodont mammal and mosaic evolution of the mammalian skeleton: Nature, v. 398, p. 326–330.

KALISZ, P.J., and DAVIS, W.H., 1992, Effect of prairie voles on vegetation and soils in central Kentucky: American Midland Naturalist, v. 127, p. 392–399.

KERMACK, D.M., 1982, A new tritylodontid from the Kayenta Formation of Arizona: Zoological Journal of the Linnean Society, v. 76, p. 1–17.

KIELAN-JAWOROWSKA, Z., CIFELLI, R. L., AND LUO, Z., 2004, Mammals from the Age of Dinosaurs: Origins, Evolution, and Structure. Columbia University Press, New York, 630 p.

KINLAW, A., 1999, A review of burrowing by semi-fossorial vertebrates in arid environments: Journal of Arid Environments, v. 41, p. 127–145.

KOCUREK, G., 2003, Limits on extreme eolian systems; Sahara of Mauritania and Jurassic Navajo Sandstone examples: Geological Society of America Special Paper, v. 370, p. 43–52.

KÜHNE, W.G., 1956, The Liassic therapsid *Oligokyphus*: Trustees of the British Museum, London, 149 p.

LAUNDRE, J.W., 1993, Effects of small mammal burrows on water infiltration in a cool desert environment: Oecologia, v. 94, p. 43–48.

LIPS, K.R., 1991, Vertebrate burrows associated with tortoise (*Gopherus polyphemus*) burrows in four habitats in south-central Florida: Journal of Herpetology, v. 25, p. 477–481.

LOCKLEY, M.G., 2005, Enigmatic dune walkers from the abyss: some thoughts on water and track preservation in ancient and modern deserts: Canyon Legacy, v. 54, p. 43–51.

LOCKLEY, M., AND HUNT, A.P., 1995, Dinosaur Tracks and Other Fossil Footprints of the Western United States: Columbia University Press, New York, 338 p.

LOCKLEY, M., YANG, S.Y., MATSUKAWA, M., FLEMING, F., AND LIM, S.K., 1992, The track record of Mesozoic birds: evidence and implications: Philosophical Transactions of the Royal Society of London, Biological Sciences, v. 226, p. 113–134.

LOCKLEY, M., HUNT, A.P., MEYER, C., RAINFORTH, E.C., AND SCHULTZ, R.J., 1998, A survey of fossil footprint sites at Glen Canyon National Recreation Area (western USA): a case study in documentation of trace fossil resources at a national preserve: Ichnos, v. 5, p. 177–211.

LOOPE, D.B., 1988, Rhizoliths in ancient eolianites: Sedimentary Geology, v. 56, p. 301–314.

LOOPE, D.B., 2006a, Burrows dug by large vertebrates into rain-moistened Middle Jurassic dunes: The Journal of Geology, v. 114, p. 753–762.

LOOPE, D.B., 2006b, Dry-season tracks in Dinosaur-triggered grainflows: Palaios, v. 21, p. 132–142.

LOOPE, D.B., 2008, Life beneath the surface of active Jurassic dunes: burrows from the Entrada Sandstone of south-central Utah: Palaios, v. 23, p. 411–419.

LOOPE, D.B., and ROWE, C.M., 2003, Long-lived pluvial episodes during deposition of the Navajo Sandstone: The Journal of Geology, v. 111, p. 223–232.

LOOPE, D.B., ROWE, C.M., AND JOECKEL, R.M., 2001, Annual monsoon rains recorded by Jurassic dunes: Nature, v. 412, p. 64–66.

LOOPE, D.B., EISENBERG, L., and WAISS, E., 2004a, Navajo sand sea near-equatorial Pangea: tropical westerlies, slumps, and giant stromatolites, *in* Nelson, E.P., and Erslev, E.A.

(eds.), Field trips in the southern Rocky Mountains, USA. Geological Society of America Field Guide 5, p. 1–13.

LOOPE, D.B., STEINER, M.B., ROWE, C.M., AND LANCASTER, N., 2004b, Tropical westerlies over Pangaean sand seas: Sedimentology, v. 51, p. 315–322.

LOUW, G.N., AND SEELY, M.K., 1982, Ecology of Desert Organisms: Longman, New York, 194 p.

LUCAS, S.G., GOBETZ, K.E., ODIER, G. P., MCCORMICK, T., EGAN, C., 2006, Tetrapod burrows from the Lower Jurassic Navajo Sandstone, Southeastern Utah: New Mexico Museum of Natural History and Science, Bulletin 37, p. 147–154.

LUO, Z.-X., CROMPTON, A.W., and SUN, A.-L., 2001, A new mammaliaform from the Early Jurassic and evolution of mammalian characteristics: Science, v. 292, p. 1535–1540.

MAGWOOD, J.P.A., 1992, Ichnotaxonomy: A burrow by any other name…?, *in* Mapes, C.G. and West, R.R. (eds.), Trace Fossils. Short Courses in Paleontology, 5, p. 15–33.

MARTIN, L.D., and BENNETT, D.K., 1977, The burrows of the Miocene beaver *Palaeocastor*, western Nebraska, U.S.A.: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 22, p. 173–193.

MAYES, P.J., 2007, The use of burrows and burrow characteristics of the semi-aquatic *Varanus mertensi* (Reptilia: Varanidae): Mertensiella, v. 16, p. 312–321.

MCKENNA, M.C., and BELL, S.K., 1997, Classification of mammals above the species level: Columbia University Press, New York, 547 p.

MILLER, M.F., HASIOTIS, S.T., BABOCK, L.E., ISBELL, J.L., and COLLINSON, J.W., 2001, Tetrapod and large burrows of uncertain origin in Triassic high paleolatitude floodplain deposits, Antarctica: Palaios, v. 16, p. 218–232.

NEVO, E., 1999, Mosaic Evolution of Subterranean Mammals: Regression, Progression, and Convergence: Oxford University Press, New York, 413 p.

NEWMAN, D.G., 1987, Burrow use and population densities of tuatara (*Sphenedon punctatus*) and how they are influenced by fairy prions (*Pachyptila turtur*) on Stephens Island, New Zealand: Herpetologica, v. 43, p. 336–344.

PARRISH, J.T., and FALCON-LANG, H.J., 2007, Coniferous trees associated with interdune deposits in the Jurassic Navajo Sandstone Formation, Utah, USA: Palaeontology, v. 50, p. 829–843.

PICKERILL, R.K., 1994, Nomenclature and taxonomy of invertebrate trace fossils, *in* Donovan S.K. (ed.), The Paleobiology of Trace Fossils: John Hopkins University Press, Baltimore, p. 3–42.

RAINFORTH, E.C., and LOCKLEY, M.G., 1996, Tracking life in a Lower Jurassic desert: vertebrate tracks and other traces from the Navajo Sandstone. Museum of Northern Arizona Bulletin, 60, p. 285–289.

REICHMAN, O.J., and SMITH, S.C., 1990, Burrows and burrowing behavior by mammals, *in* Genoways, H.H. (ed.), Current Mammalogy: Plenum Press, New York, p. 197–244.

SEILACHER, A., 1992, Quo vadis, ichnology?, *in* Mapes, C.G. and West, R.R. (eds.), Traces Fossils: Short Courses in Paleontology, 5, p. 224–238.

SEILER, W.M., and CHAN, M.A., 2008, A wet interdune dinosaur trampled surface in the Jurassic Navajo Sandstone, Coyote Buttes, Arizona: rare preservation of multiple track types and tail traces: Palaios, v. 23, p. 700–710.

SIDOR, C.A., MILLER, M.F., and ISBELL, J.L., 2008, Tetrapod burrows from the Triassic of Antarctica: Journal of Paleontology, v. 28, p. 277–284.

SMITH, R.M.H., 1987, Helical burrow casts of therapsid origin from the Beaufort Group (Permian) of South Africa: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 60, p. 155–170.

SUES, H.-D., 1984, Inferences concerning feeding and locomotion in the Tritylodontidae (Synapsida), *in* Reif W.-E., and Westphal, F. (eds.), Third Symposium on Mesozoic Terrestrial Ecosystems Short Papers: Tübingen University Press, Tübingen, p. 231–236.

SUES, H.-D., 1985, First record of the trityolodontid *Oligokyphus* (Synapsida) from the Lower Jurassic of western North America: Journal of Vertebrate Paleontology, v. 5, p. 328–335.

SUES, H.-D., 1986a, *Dinnebitodon amarali*, a new tritylodontid (Synapsida) from the Lower Jurassic of western North America: Journal of Paleontology, v. 60, p. 758–762.

SUES, H.-D., 1986b, The skull and dentition of two tritylodontids synapsids from the Lower Jurassic of western North America: Bulletin of the Museum of Comparative Zoology at Harvard College, v. 151, p. 217–268.

SUES, H.-D., CLARK, J.M., and JENKINS, JR. F.A., 1994, A review of the Early Jurassic tetrapods from the Glen Canyon Group of the American Southwest, *in* Fraser N.C. and Sues H.-D. (eds.), In the Shadow of the Dinosaurs: Early Mesozoic Tetrapods: Cambridge University Press, New York, p. 284–294.

TANNER, L.H., AND SMITH, D.L., and LUCAS, S.G., 2006. Trace fossils in eolian facies of the Upper Triassic-Lower Jurassic Dinosaur Canyon Member, Moenave Formation, Northern Arizona. Ichnos, 13:21–29.

TAYLOR, H.M., 1971, Root behavior as affected by soil structure and strength, *in* Carson, E.W. (ed.), The Plant Root and its Environment: University of Press Virginia, Charlottesville, p. 271–291.

VLECK, D., 1981, Burrow structure and foraging costs in the fossorial rodent, *Thomomys bottae*. Oecologia, v. 49, p. 391–396.

VOORHIES, M.R., 1975a, Vertebrate burrows, *in* Frey, R.W. (ed.), The study of trace fossils: Spring-Verlag, New York, p. 325–350.

WINKLER, D.A., JACOBS, L.L., CONGLETON, J.D., AND DOWNS, W.R., 1991, Life in a sand sea: biota from Jurassic interdunes: Geology, v. 19, p. 889–892.

CHAPTER 4. A REVIEW OF ANCIENT AND EXTANT VERTEBRATE BURROWS MORPHOLOGIES

ABSTRACT

Burrowing is a behavioral adaptation of animals in response to environmental conditions. Burrows are used for living, feeding, brooding, or temporary refuge from extreme conditions or predators. Modern vertebrates that commonly excavate burrows comprise fish, amphibians, reptiles, and mammals. Fossil burrows are also known from vertebrates, including the extinct order Therapsida. Lungfish burrows in Devonian fluvial deposits are the earliest known record of vertebrate burrowing. Burrow morphologies reflect the tracemaker's anatomy, social structure, media consistency, and food availability. Some morphologies are consistent within the major groups in both fossil and extant vertebrates. The number of fossil vertebrate burrows identified has increased recently. Fossil burrows are described and identified most commonly by their architectural and surficial morphologies. Although there are reviews on burrows of individual groups of vertebrates, there are few compilations of these morphologies into a single review. This review of vertebrate burrow morphologies is important as it can be used to more accurately identify enigmatic structures in the fossil record, and help distinguish biogenic and from abiogenic structures.

INTRODUCTION

This paper presents a review of ancient and extant vertebrate burrow morphologies with descriptions and drawings and identifies the similar burrow morphologies within the major vertebrate groups examined. This review will allow for easier identification of burrows and their tracemakers, as well as their identification from abiogenic origins with grossly similar

morphologies. Previous reviews have focused on modern subterranean mammals burrows and their uses (Hickman, 1990; Reichman et al., 1990; Nevo, 1999). Reviews of fossil vertebrate burrows have been published in the past by Voorhies (1975) and Hasiotis et al. (2007).

Modern vertebrate burrows are predominately found in continental environments, but are also found in aquatic environments. These burrows are used for protection, mating, food gathering, aestivation, hibernation, and dwelling (Kinlaw, 1999; Hasiotis, 2002; Hasiotis et al., 2007). Architectural morphologies of vertebrate burrows can vary for a variety of reasons that include anatomy, social structure, media consistency, food availability, and the burrowing behavior itself (e.g., Davies and Jarvis, 1986; Jarvis and Sale, 1971; Spinks et al., 2000).

Fossil vertebrate burrows were once thought to be rare because fossorial habits among vertebrates were limited compared to modern vertebrates, and the preferred environments for excavating burrows are not well preserved in the stratigraphic record (Voorhies, 1975). Fossil vertebrate burrow discoveries has increased recently, and are recognized in continental and aquatic strata as old as the Devonian (e.g., Martin and Bennett, 1977; Hunt et al., 1983; Smith, 1987; Groenewald et al., 2001; Miller et al., 2001; Damiani et al., 2003; Hasiotis, 2002; Hasiotis et al., 1999; 2004, 2007; Hembree et al., 2004, 2005; Gobetz, 2006; Gobetz and Martin, 2006; Loope, 2006a, 2008; Hembree and Hasiotis, 2006, 2008, Lucas et al., 2006; Riese et al., 2011).

Fossil burrows are described based on their architectural and surficial morphologies, and are predominately identified by comparisons to extant vertebrate burrows (Smith, 1987; Groenewald et al., 2001; Miller et al., 2001; Hasiotis et al., 2004, 2007; Loope, 2006). The excavator of fossil burrows can also be identified by body fossils (Romer and Olson, 1954; Carlson, 1968; Voorhies, 1974, 1975a; Olson and Bolles, 1975; Dalquest and Carpenter, 1977; Martin and Bennett, 1977; Hunt et al., 1983; Smith, 1987; Hasiotis et al., 1993; Groenewald et

al., 2001; Damiani et al., 2003). The body fossil record has lower fossilization potential then the burrows and, therefore, burrows represent a hidden biodiversity in the fossil record when body fossils are not present in those rocks (Hasiotis and Bourke, 2006; Hasiotis et al., 2007). Identifying the excavator can also be complicated by organisms other than the original excavator occupying the burrow, as is often seen in modern burrows (Norris, 1953; Auffenberg and Weaver, 1969; Voorhies, 1975). Fossil vertebrate burrows represent an interaction between the organism and the media illustrating one or multiple behaviors. Modern burrows can be considered homologs and analogs to fossil vertebrate burrows and, therefore, were likely used for the same behavioral and physiological reasons of modern burrows owing to ecological and environmental reasons (Hasiotis and Bourke, 2006). Fossil burrows can also provide information on pre- and postdepositional histories of the environment (Hasiotis et al., 2007).

The burrow morphologies of fish, amphibians, reptiles, therapsids, and mammals are reviewed. Each section discuss extant and, if possible, fossil burrows of orders, classes, or families within the major groups. Where possible a description of burrow comparisons is done to show minor differences in burrow morphologies between different groups. A summary of the important architectural morphologies that can aid in identification of that group is provided at the end of each section. A discussion of the potential for future research and expanding on this review is also provided.

Terminology

Architectural morphology of burrows includes the diameter (width and height), length of each segment, type (Y, T) and angle of branching, orientations, burrow shapes, and area dimensions. Architectural morphology also includes the complexity and connectivity of

structures. Horizontal burrows are termed tunnels, inclined tunnels are ramps, and vertical burrows are shafts. A ramp that spirals around a reference axis is a helical burrow. Chambers are enlarged areas that can be found at the end of a shaft or tunnel in which case are termed terminal chambers, or can be found within the tunnel, shaft, or ramp. Surficial morphology includes scratches, ridges, or knobs that record the excavation or locomotion methods used to construct or maintain the burrow (Fig. 30).

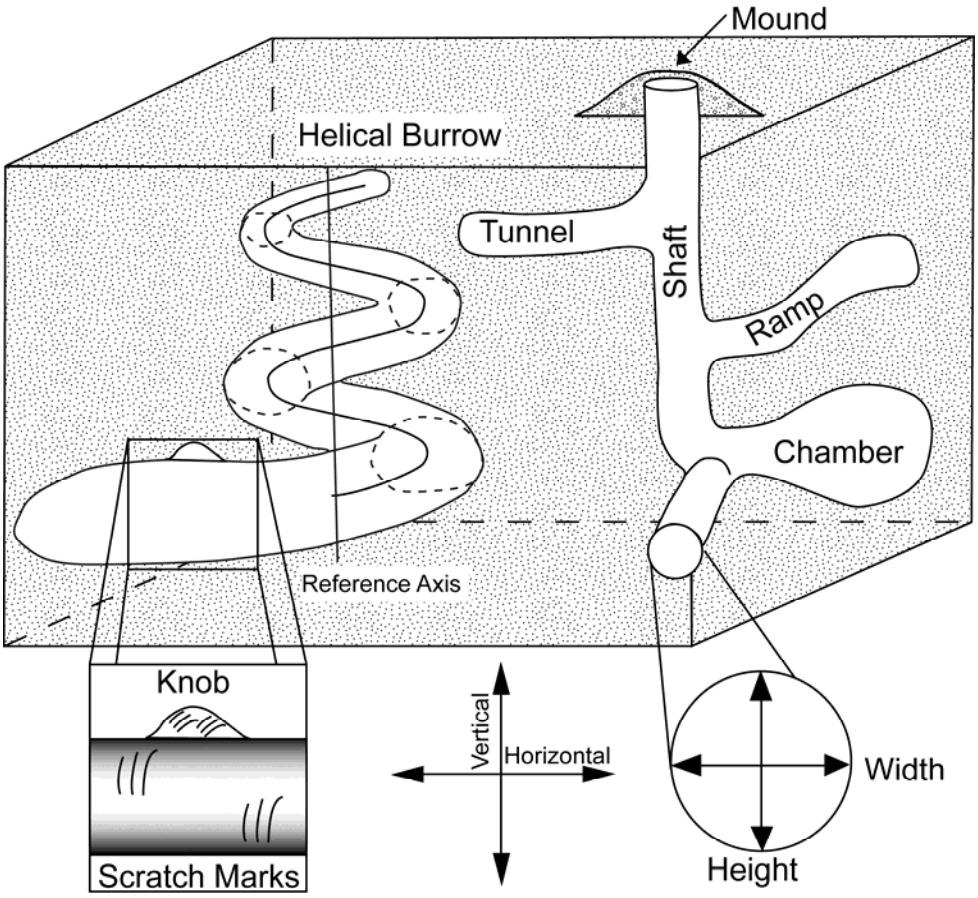

FIGURE 30—Common terms used to describe architectural and surficial morphologies of burrows. Modified from Hasiotis et al. (2007).

FISH BURROWS

Fish live in aquatic environments, and include the jawless, cartilaginous, ray-finned, and lobe-finned fish. Fish most often excavate burrows using the mouth, as well as body undulations and movements. The burrows are predominately used for protection from predators, but are also used to escape desiccation in areas that experience wet and dry seasons that reduce the size of water bodies (e.g., Bouillon, 1961; Atkinson and Taylor, 1991).

Sarcopterygii

Extant lungfish burrows.—Modern lungfish live in South America, Africa, and Australia in freshwater muddy areas that experience wet and dry seasons (Romer and Olson, 1954, McAllister, 1988). The South American and African lungfish have adapted the ability to use burrows as aestivation chambers when there is either a lack of water or extreme temperatures by initiating a state of inactivity and lower metabolism (Romer and Olson, 1954; Atkinson and Taylor, 1991; Hasiotis et al., 2007).

Aestivation burrows of *Protopterus* from Africa are mucus-lined shafts that end in a widened chamber (Johnels and Svennsson 1954; Greenwood, 1986) (Fig. 31A). The diameter and depth of the shaft varies depending on the size of the lungfish, but burrows measured by Johnels and Svennsson (1954) ranged from 0.5 to 7 cm wide and 3 to 25 cm long from the entrance to the top of the chamber. An earthen cap that is usually a different color than the surrounding sediment covers shafts at the surface. The chamber generally widens towards the rounded bottom, and is greatest just above the lower end. The longitudinal axis of the cross section is on average twice as long as the diameter of the shaft leading to the chamber, and the short axis is equal to the diameter of the shaft (Johnels and Svensson, 1954).

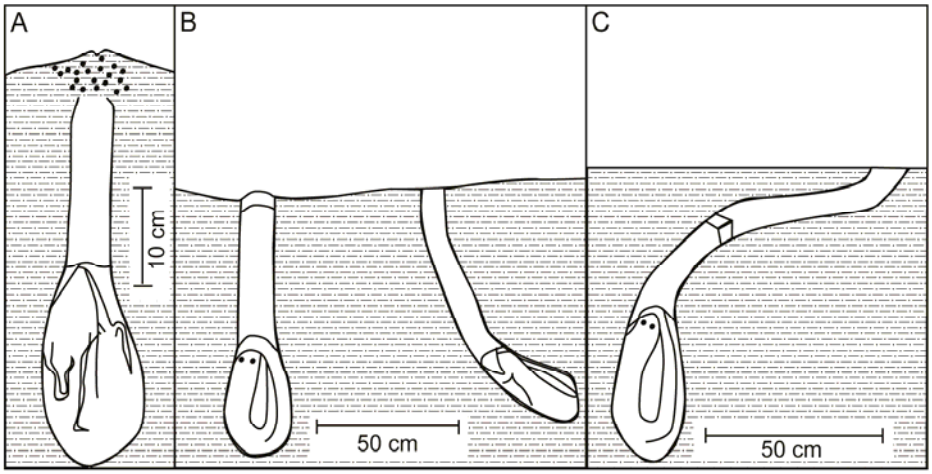

FIGURE 31—Architecture of lungfish burrows with lungfish inside. A). Burrow of *Protopterus annectens*. Notice cap of the entrance and cocoon. Modified from Johnels and Svensson (1954). B–C). Burrows of *Lepidosiren.* Modified from Kerr (1898).

Aestivation burrows of *Lepidosiren* from South America are vertical to subvertical shafts that terminate in an oblong chamber where the lungfish is in a curled position (Kerr, 1898; Carter and Beadle, 1930) (Fig. 31B–C). The diameter and depth of the aestivation burrows will vary depending on the size of the lungfish with diameters ranging 6 to 8 cm and tunnels 30 to 91 cm in length. The shaft entrance is plugged with mud, and often several plugs are found in a long tunnel (Kerr, 1898; Carter and Beadle, 1930). The chamber at the end of the shaft is oblong in shape with an average diameter of 35.6 by 15.2 cm (Kerr 1898). There is no evidence of a mucus lining within the shaft or chamber (Kerr, 1898; Carter and Beadle, 1930).

Fossil lungfish burrows.—Fossilized lungfish burrows excavated by members of the *Gnathorhizidae* were found by Romer and Olson (1954) in the Permian Clear Fork Group of Texas. Gnathorizid burrows are abundant in the fossil record, and are found dating back to the Devonian Period (Hasiotis, 2002; Jones and Hasiotis, in review). Fossilized lungfish burrows are identified unambiguously when lungfish remains are found encased within them (McAllister,

1988). The burrowing method of *Gnathorhizidae* is thought to be similar to that of modern lungfish based on comparisons of architectural and surficial morphologies in association with the burrowing mechanisms of modern lungfish (Hasiotis et al., 2003).

Gnathorhizid burrows are simple and rarely deviate in morphology. The burrows are vertical shafts with circular to elliptical cross sections that vary from 1 to 10 cm in diameter and 10 to 50 cm long, or flask-shaped with an upper cylindrical portion and a bulbous termination (Romer and Olson, 1954; Carroll, 1965; Hasiotis et al., 1993; Hasiotis et al., 2007). Burrows have distinct sides and bottoms, but indistinct tops (McAllister, 1988; Hasiotis et al., 2007). The surficial morphology of the burrows is predominately smooth; however, few burrows contain small nodes or subhorizontal to subvertical striations interpreted as scale or fin scratches and nose prod marks (Carroll, 1965; Hasiotis et al, 1993; Hasiotis et al., 2007). Lungfish burrows indicate that the paleoenvironment experienced a dry period where rivers and lakes may have dried up seasonally. Crosscutting burrow structures associated with rhizoliths and pedogenic structures indicates a repeated series of wet and dry conditions with pedogenesis taking place when aquatic settings become subaerial (Carlson, 1968).

Actinopterygii

Extant Actinopterygii burrows.—The burrow of the gobiid fish *Lesueurigobius friesii* comprises a main tunnel that is U-shaped with two entrances to the surface with the main entrance the larger of the entrances (Rice and Johnstone, 1972). Some burrows have three openings (Fig. 32A–B). The inner edges of the two surface entrances are ~20 cm apart, and the tunnels incline ~30° and level out at a depth of ~9 cm. The main tunnel has a side branch of variable size and form. One side branch described by Rice and Johnstone (1972) is 18 cm long

that ends in a narrow vertical shaft with a small opening on the surface (Fig. 32A). Smaller side branches may not have an opening to the surface. One burrow that was occupied by two gobies in separate parts of the burrow is more complex with long multibranched tunnels with several openings (Fig. 32C). Crabs, however, may have originally excavated the complex burrows, because the crab burrows share many similarities with the burrows the goby fish occupied.

Boleophthalmus boddarti live in polygonal territories of various size and shapes, which are separated by mud walls (Clayton and Vaughan, 1986). The burrows found within the territories comprise a main burrow entrance that leads to a shaft 1–2 m deep, and at least one side entrance. Some of the burrow entrances can be blocked by sediment (Fig. 32D–F).

The burrow of the yellowhead jawfish *Opistognathus aurifrons* has three morphologies resulting from different media conditions (Colin, 1973). The opening of the burrows are ~1.4–2 cm, and burrows are 11–22 cm deep; a few are deeper, however. The first type of burrow morphology occurs where a burrow is started adjacent to a rock or a rock is encountered during excavation. A terminal chamber is constructed underneath the rock with multiple branches originating from the chamber. The second type of burrow is a terminal chamber that is lined with large coral fragments, but not roofed with a rock (Fig 32G). The initial construction of this burrow morphology begins with excavation of a pit, ~ 20 cm in diameter and 15 cm deep at its largest. The pit is infilled with rocks for stability that creates a roof allowing the fish to extend the burrow to create a terminal chamber. The third burrow morphology has a terminal chamber in an erosion hole or in a fracture of a buried rock.

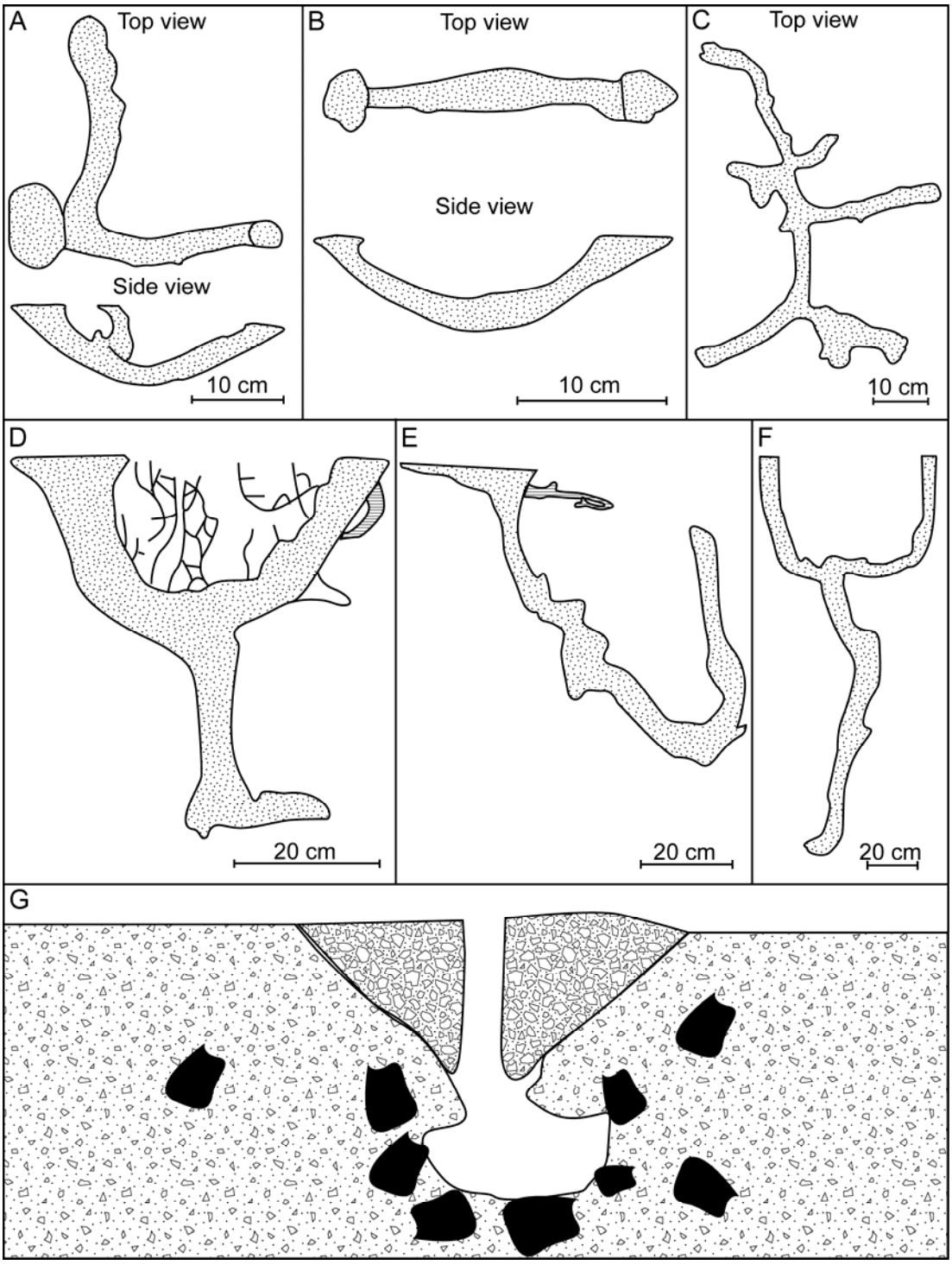

FIGURE 32—Architecture of fish burrows. A). Top and side view of a *Lesueurigobius friesii* burrow. B). Top and side view of an *L. friesii* burrow constructed in an aquarium. C) Top view of a *L. friesii* burrow occupied by two gobies that used separate parts of the burrow. This burrow

may have been originally excavated by crabs. Modified after Rice and Johnstone (1972). D). *Boleophthalmus* burrow with two entrances. Note towards the top of the burrow the smaller crab burrows viewed as black lines as well as different fill pattern then the main burrow. E). *Boleophthalmus* burrow with one entrance also with crab burrow located near the entrance. F). *Boleophthalmus* burrow with two entrances. Modified from Clayton and Vaughan (1986). G). Second burrow morphology of the yellowhead jawfish *Opistognathus aurifrons*. Note the stones within the pit creating stability, and the material surrounding the terminal chamber. Modified from Colin (1973).

The chamber size of all burrows varies with maximum dimensions of 24 cm long, 23 cm wide, and 6 cm high. One burrow had two chambers, one lying directly underneath the other and connected by a tunnel 24 cm long that extended out and then reversed direction to the lower chamber. One burrow also had two closely spaced entrances with tunnels only a few centimeters long that converged into one tunnel.

The burrow of the red band fish *Cepola rubescens* comprises a funnel entrance that leads to an elliptical shaft that enlarges to a chamber at the base (Atkinson et al., 1977; Atkinson and Pullin., 1996) (Fig. 33A–B). In one study the burrow diameter at the entrance ranged from 1–22 cm, and averaged 9.1 cm (Atkinson and Pullin, 1996). In another study the average burrow diameter at the surface is 10 cm. These burrows 10–15 cm below the surface became narrower with an average diameter of 6 cm for ~38 cm until it opened up to a terminal chamber with an average maximum diameter of 11 cm that extends for an average distance of 24 cm (Atkinson et al., 1977). Some burrows are deflected laterally 30–50° from horizontal (Fig. 33A). Smaller burrows have a side branch that did not always have an entrance to the surface (Fig. 33A). In one

study burrows extended to an average depth of 49 cm, but ranged from 5–94 cm, and in another study the average depth was 64 cm (Atkinson et al., 1977; Atkinson and Pullin, 1996). Burrow complexity is predominately based on interconnection with crab and callianassid shrimp burrows (Atkinson and Pullin, 1996) (Fig. 33B).

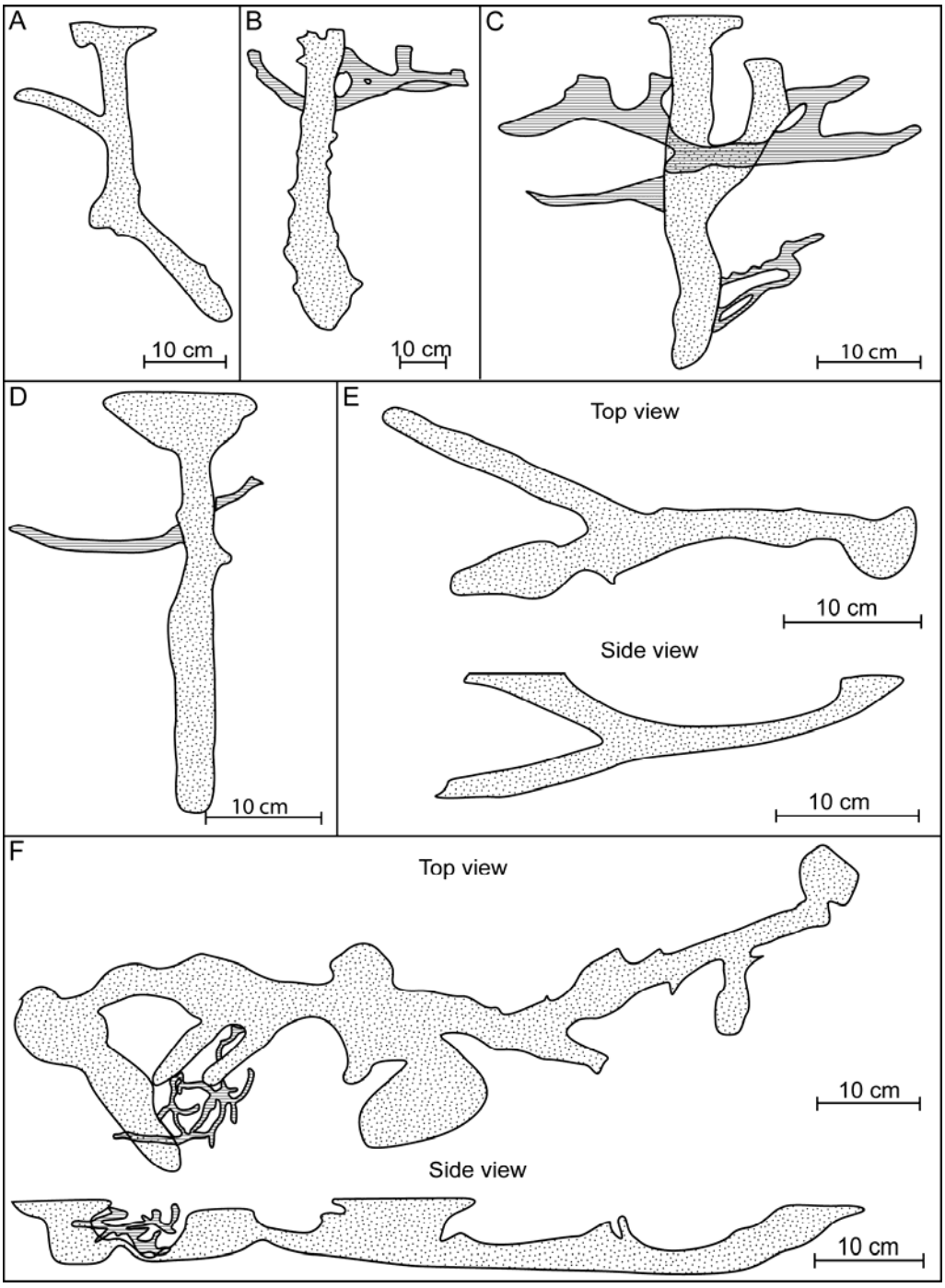

FIGURE 33—Architecture of fish burrows. Burrows with other fill pattern excavated by crabs. A). Architecture of the red band fish *Cepola rubescens* burrows with a branch that does not reach the surface and a lateral deflection towards the base. Modified from Atkinson and Pullin (1996). B). Vertical *C. rubescens* burrow with interconnecting crab burrows near the entrance. Modified from Atkinson et al. (1977). C). *Lonchopisthus micrognathus* burrow with a main opening and a secondary opening to the right. D). *L. micrognathus* burrow without any secondary opening. Modified from Colin and Arneson (1978). E). Top and side view of *Lumpenus lampretaeformis* burrow. Burrow has two openings with third side tunnel not does reach the surface. F) Top and side view of a more complex *L. lampretaeformis* burrow. Modified from Atkinson et al. (1987).

The burrow of the swordtail jawfish *Lonchopisthus micrognathus* has a shaft that tapers towards the central portion, and has an expanded terminus (Colin and Arneson, 1978) (Fig. 33C–D). The smallest diameter of the shaft is 2.5–5 cm. The burrows reach a depth of 17–35 cm, though some may reach as far as 50 cm. The burrows are not lined with any stones or shell fragments. In most burrows a secondary tunnel is excavated several centimeters below the main opening which goes a short distance horizontally, and then curves upward reaching the surface as a secondary opening (Fig. 33C). The secondary opening is smaller and not conical like the primary opening. Crab burrows found with the *L. micrognathus* burrows are horizontal meandering tunnels (Fig. 33C).

The burrows of the snake blenny *Lumpenus lampretaeformis* have varying complexity (Atkinson et al., 1987) (Fig. 33E–F). The typical burrow had three openings, with two main openings and a third opening to the surface that can be open and closed (Fig. 33E). At times the smaller side branch comes within 2 cm of the surface, and resembles the shape and dimensions

of the fish. The cross section of tunnels ranged from subtriangular to circular with dimensions ranging from 1.1–2.1 cm high and 1.6–3.2 cm wide. The burrows are generally shallow, inclined at 30–50° and extend horizontally. The average maximum depth of the burrow is 7.2 cm. At times the roof of the tunnels are just below the surface at an average depth of 3.6 cm, but was a little has 0.7 cm. Burrow lengths range from 20–35 cm, with a maximum of 73 cm (Fig. 33F). Side branch junctions are Y-shaped with an oval cross section and dimensions ranging from 1.9–4.0 cm high and 4.0–7.3 cm wide with an average smaller branch angle of 62°. In the laboratory setting, 12 *L. lampretaeformis* were allowed to burrow in a tank, and they created a complex interconnecting burrow system. The burrows had many similarities of those excavated by individuals. Differences in the burrow complexes are that they are expanded laterally in middle sections, especially around burrow junctions. Burrows also have expanded areas both laterally and vertically thought to be used for turning around.

Summary

Extant fish burrows morphologies are simple in architecture consisting of vertical to horizontal burrows. Tunnels and shafts predominately have elliptical to circular cross sections. The size and depth of burrows depended on such factors as the size of the fish and the use of the burrow. Vertical burrows typically have an opening to the surface that leads to a shaft that ends in a widened terminal chamber (Figs. 31A–C; 32D–G; 33A–D). Vertical burrows can also have a secondary tunnel that is typically smaller then the main shaft, and either stops short of the surface or is a secondary opening (Fig. 32D, F; 33A, C). Horizontal burrows are predominately J or Y-shaped with 2–3 entrances to the surface (Fig. 32A–B; 33E-F). Horizontal burrows can also

have an additional tunnel that is smaller then the main shaft, and stops short of the surface or is another opening (Fig. 32A, 33E–F).

Fossil fish burrows are likely to have similar morphologies to their modern counterparts. The similar morphologies would be produced because of the same basic body plan, same environments, and similar lifestyles between fossil and extant fish. A well-documented example of a group of fish with similar morphologies between the fossil and extant groups is lungfish. Lungfish burrows throughout time are generally constructed as vertical burrows that have an opening to the surface that leads to a shaft that ends in a widened terminal chamber.

When fossil fish burrows are found they would likely be simple in architecture consisting of vertical or horizontal tunnels with two or three side branches. A key identification tool when trying to identify fish burrows is looking at the surrounding rocks to identify the paleodepositional environment. Fish burrows are going to be found in either marine, lacustrine, or even fluvial environments.

AMPHIBIAN BURROWS

Amphibians have been around since the late Devonian, and live in both freshwater and terrestrial habitats; some are completely terrestrial, whereas others are completely aquatic. Amphibians lay their eggs in water, and then later the larvae metamorphose to a land-dwelling form. Modern amphibians include salamanders, frogs, and caecilians (Carroll, 1988; Stebbins and Cohen, 1995). Modern amphibians burrow into sediments to control water regulation, and also for responses to cold weather (Pinder et al., 1992). In drying conditions amphibians will often burrow into the sediment, hide in natural openings, or seek out other animals burrows to avoid desiccation (Smith, 1956; Stebbins and Cohen, 1995). Caecilians are limbless, wormlike

amphibians that are the most suited for a fossorial lifestyle. Most of these organisms burrow into damp soil or decayed wood, though some are aquatic (Stebbins and Cohen, 1995). Most literature on caecilian burrows does not discuss their burrow morphologies, but focus on the functional morphology of the caecilian body or burrowing methods (e.g. Gans, 1973; Ducey et al., 1993).

Anurans

Extant anuran burrows.—Burrowing is common among the anura (frogs) with some that burrow only occasionally, others spending long periods of time underground only to surface for feeding and breeding, others are completely subterranean, and others have been known to occupy burrows of other organisms (Emerson, 1976; Ruibal and Hillman, 1981; Pinder et al., 1992). Burrowing is known to occur in the Bufonidae, Rhinophrynidae, Pelobatidae, Hylidae, Ranidae, Myobatrachidae, Microhylidae, and Leptodactylidae, and more than 95% dig hindfeet first into the soil (Hildebrand, 1974; Emerson, 1976; Pinder et al., 1992). Frogs of the Leptodactyllidae and Scaphiopodidae that live in periodically dry habitats often aestivate within soil or mud and can form a cocoon to survive the adverse environment. Many of the aestivating anurans are highly terrestrial, though some are aquatic (Lee and Mercer, 1967; McClanahan et al., 1976; Pinder et al., 1992).

Anuran burrows are simple to complex in architecture and comprise a single opening to the surface with initial segments inclining at angles ranging from horizontal to vertical, though some burrows collapse behind the frog (Pinder et al., 1992; Penna and Solís, 1996; 1999) (Fig. 34). Initial segments can be connected to long underground galleries (Penna and Solís, 1996). Frogs excavating into loose soil tend to excavate deeper tunnels when the dry or winter season

approaches, though frogs excavating into harder soils cannot excavate deeper (e.g., Bragg, 1944; Pinder et al., 1992). *Scaphiopus* excavates to ~20 cm in the fall and 50–70 cm in the winter, whereas burrows excavated for daytime use during summer seasons are 6–8 cm. Other genera have excavated burrows to >150 cm (Pinder et al., 1992).

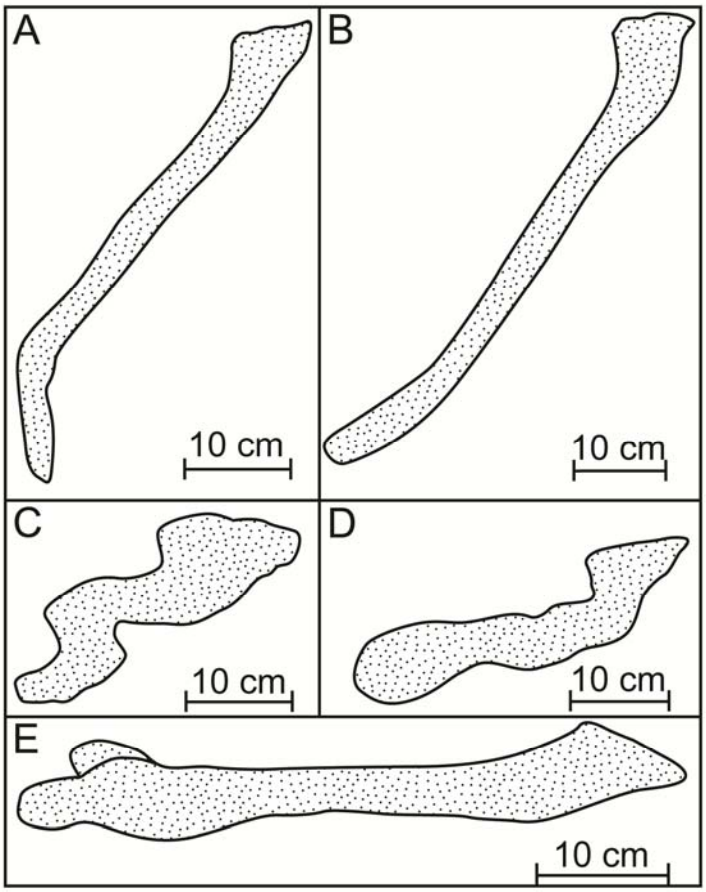

FIGURE 34—Burrow morphologies of 5 species of *Heleioporus*. Top line of burrow in each part represents the surface line. A). *H. psammophilus*; B). *H. eyrei*; C). *H. inornatus*; D). *H. barycragus*; E). *H. albopunctatus*. Modified from Bailey and Roberts (1981).

Caudata

Extant caudate burrows.—The caudata (salamanders) burrow mainly for aestivation and are simple in architecture. Many salamanders also use natural crevices or burrows of other animals (Stebbins and Cohen, 1995). Aestivation has been reported in individuals of the Amphiumidae, Sirenidae, Plethodontidae, and Ambystomatidae (Pinder et al., 1992). Aestivating salamanders belonging to the family Sirenidae were found in burrows within a pond (Freeman, 1958). Two of the amphibian's burrows are the diameter of the amphibian's body, one a shaft connecting to the surface, and the other a horizontal tunnel slightly longer than the amphibian's body 4 cm below the surface with no visible connection to the surface. Several amphibians were found in S-shaped tubes slightly longer than their bodies, with only one tube extending to the surface. Some salamanders that aestivate wrap themselves within cocoons (Reno et al., 1972). Some salamanders configure themselves so that most of its surface area is in direct contact with the soil (Etheridge, 1990).

Lysorophidae

Fossil Lysorophid burrows.—The Lysorophidae is a family of ancient amphibians from the Carboniferous to the Permian Period (Carroll, 1988). Lysorophid burrows normally have elliptical cross sections with dimensions ranging from 1–8 cm. The burrows are oriented vertically but can deviate up to 40° and taper downward with a maximum burrow length of 32 cm, but are normally 10–15 cm long. Surficial morphologies predominately comprise irregularly spaced nodes created from the snout. Permian burrows with *Lysorophus* specimens reveal two or three quasi-horizontal striae that occur in single sets that do not intersect with other sets or curve upward (Hasiotis et al., 1993). Burrows normally have an indistinct top, but sides and bottoms

show a boundary from the surrounding medium marked by a change in lithology, grain size, and color (Hembree et al., 2004).

The lysorophid *Brachydectes elongates* are found associated with burrows in the Lower Permian Speiser Shale of eastern Kansas (Hembree et al., 2004). The burrows are assigned to the ichnotaxon *Torridorefugium eskridgensis* (Hembree et al., 2005). Two types of architectural morphologies are described that are different owing to the size of the organism and the nature of the medium (Fig. 35). The first type comprises mostly vertical, elongate, narrow elliptical tubes, with a width-to-length ratio <1 (Fig. 35A–B). Burrows ranged from 2.5–32 cm long with maximum upper diameters from 2–7 cm. These burrows taper irregularly downward from broad upper surfaces to a conical and rounded burrow termination. A slight deviation from vertical orientation is created from a sinuous architecture occurring at the midpoint of the burrow. The surficial morphology of these burrows comprises irregularly spaced nodes.

The second type of architectural comprises short, broad elliptical tubes with width-to-length ratios >1 (Fig. 35C). Burrows ranged from 1.5–5.0 cm long with maximum upper diameters ranging from 2.5–6.0 cm. These burrows taper slightly less than the first type and do not exhibit any surficial morphology. In some areas a reduction halo extends several cm from the burrow. Burrow concentrations ranged from $1/m^2$ to $20/ m^2$ with all sizes intermixed except in one layer where smaller burrows tended to occur on the fringe of the area (Hembree et al., 2004; 2005).

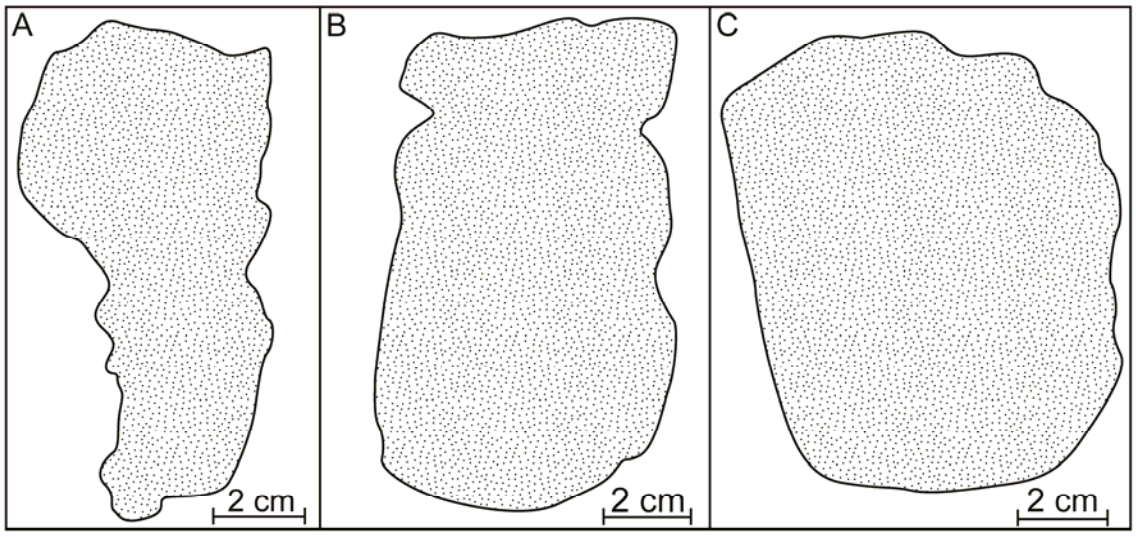

FIGURE 35—Architecture of lysorophid burrows. A–B). Type I architectural morphology. C). Type II architectural morphology. Modified from Hembree et al. (2004).

Summary

The morphology of ancient and extant amphibian burrows is predominately simple (Fig. 34–35). The burrow morphology of some frog burrows is more complex consisting of simple initial tunnels that lead to underground galleries. The overall morphology of modern amphibian burrows can be horizontal to nearly vertical consisting of a simple tunnel. Burrow depth varies on the type, size, and season of burrowing but could be >150 cm with frog burrows. Several salamanders and frogs (i.e., family Sirenidae and Leptodactylidae) can form cocoons to survive drying conditions. Fossil lysorophid burrows are vertically oriented, but can deviate up to 40°. Lysorophid burrows superficially resemble lungfish burrows but differ because they typically taper downward, are not as long, and comprise large, irregularly spaced nodes on burrow walls (Fig. 35).

REPTILE BURROWS

The class Reptilia is characterized by a cold-blooded metabolism, laying amniotic eggs, and skin usually covered in scales or scutes (Carroll, 1988). Reptilia comprise four extant orders, Testudines, Crocodilia, Sphenodontia, Squamata, all of which are known to excavate burrows (Voorhies, 1975). The earliest evidence of reptiles is from tracks within Carboniferous deposits in Nova Scotia (Falcon-Lang et al., 2007). Reptiles that excavate burrows include those that excavate a permanent burrow (e.g., monitor lizard, gopher tortoise), search for food in loose sand (e.g., snakes), are permanent fossorial foragers (e.g., amphisbaenians), and dig deep nests for brooding (e.g., crocodiles, turtles). The trace fossil record of reptile burrows is poor (Voorhies, 1975).

Testudines

Extant Testudine.—*Gopherus*, the gopher tortoise, is one group that excavates burrows. The architecture of *Gopherus polyphemus* burrows are generally simple comprising a long subhorizontal tunnel with one or two curves, but burrows predominately curve to the right (Hallinan, 1923; Hansen, 1963; Auffenberg and Weaver, 1969) (Fig. 36). The angle of inclination of tunnels ranged from 15–45° with an average of ~27° (Hallinan, 1923; Hansen, 1963). The burrows have a hemispheric cross-sectional shape owing to the shape of the carapace, and the burrow width is usually twice as large as the height; the maximum dimensions are 28 cm wide and 15.2 cm high (Hallinan, 1923). Burrow dimensions are larger at the burrow entrance then further down within the burrow (Hansen, 1963). At the entrance the burrows dimensions range from 18.5–30.4 cm wide and 6.3–16.5 cm high. Sixty one cm below the burrow entrance

the dimensions ranged from 13.4–24.1 cm wide and 6.3–14 cm high, and averaging 17.8 cm wide and 8.9 cm high. Dimensions of burrows in other studies range from 25–35 cm wide and 11–18 cm high (Kinlaw et al., 2007). The burrow lengths of gopher tortoises in other studies range from 3–12.2 m. The burrow lengths vary from 1.9–14.5 m with an average of 4.6 m, and there is a strong correlation between the tortoise size, burrow width and height, and the length of the burrows (Hansen, 1963). The greater the tortoise size and larger dimensions of the burrows, the longer of the burrow lengths are generally. The vertical depth of the burrow systems ranged from 1.4–2.8 m and average 2 m (Hansen, 1963).

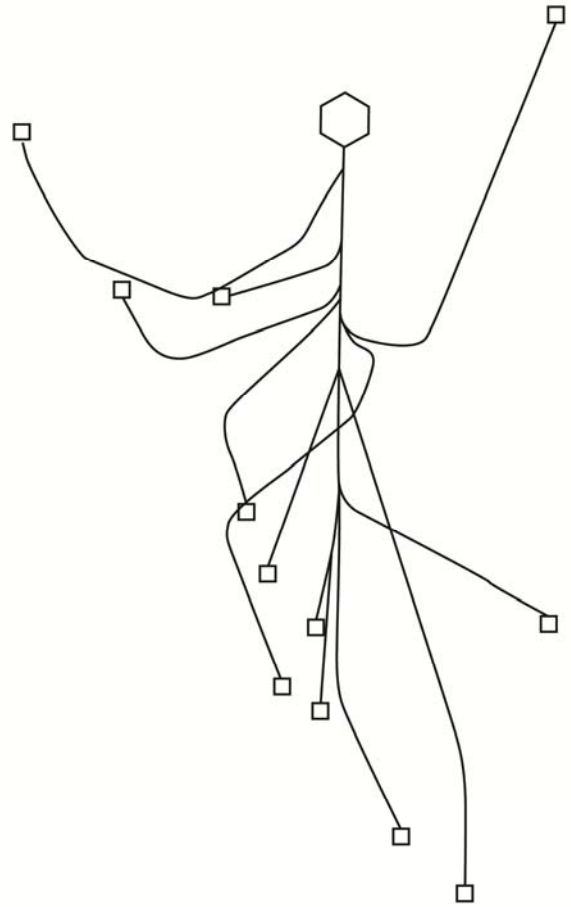

FIGURE 36—Plan view showing direction of 12 gopher tortoise burrows. Each burrow is a separate tunnel. Modified from Hallinan (1923).

Crocodilia

Extant crocodilian.—The crocodilians include crocodiles, alligators, gharial, and caiman families. Crocodilians generally create nests for brooding; however, they have also excavated burrows for hibernation (Pooley, 1969; Neill, 1971; Voorhies, 1975). The American alligator often excavates burrows in areas seasonally inundated by water, such as the pine flatwoods that have a hard clay pan or in floodplains of large rivers (Neill, 1971). The Nile crocodile excavates riverbank burrows in drier parts of its range (Voorhies, 1975). A burrow is generally composed of a long horizontal tunnel that opens into an enlarged chamber. The burrow diameter is not much greater than the excavator (Neill, 1971). Poole (1969) who was documenting the burrowing behavior of 1 year old crocodiles 61–91.4 cm long, found burrows ranging from 1.2–3.6 m long. Burrows of other crocodiles can reach lengths of 12 m (Voorhies, 1975). The burrows also can have short side branches that represent old burrow paths before that terminated when an obstacle was encountered (Neill, 1971).

Fossil crocodilian.—Hasiotis et al. (2004) interpreted burrows in the middle part of the Salt Wash Member of the Upper Jurassic Morrison Formation to be reptilian, and they appear similar in morphology to crocodiles, sphenodontids, or turtles. These burrows are simple in architecture comprising subhorizontal tunnels with inclinations ranging from 5–25° from the paleosurface. The cross sections of the burrows are elliptical with maximum diameters ranging from 15–50 cm, and lengths can be >200 cm. Burrow terminations, when visible, are slightly wider than the burrow diameter. On the burrow walls and floors are a series of scratch marks that range from 0.3–25 cm long. The burrows are found in channel margin, levee, and proximal floodplain environments that show no pedogenic formation. The lack of pedogenic formation

and undisturbed primary sedimentary structures suggests that there were relatively high-water tables and sedimentation rates. The reptiles, therefore, likely excavated burrows in areas of damp conditions.

Sphenodontia

Exant Sphenodontia.—The Sphenodontia have a body fossil record known from the late Triassic with only one living genus the *Sphenodon* (tuatara) found on ~35 offshore islands of New Zealand (Fraser, 1988; Gillangham et al., 1995; MacAvoy et al., 2007). Tuataras are generally active at night, and spend their days in burrows (Mulder and Keall, 2001).

The tuataras are often found sharing burrows with a type of bird called fairy prions—who are the excavators, though tuataras are known to excavate burrows themselves (Voorhies, 1975; Newman, 1987; Mulder and Keall, 2001). Most studies on tuatara burrows are of those that are shared occupancies. The tuataras occupy several different burrows, and several tuataras can also use the same burrow at different times. Tuataras occupy both simple and complex burrows (Newman, 1987). Simple burrows are recognized based on one or two surface openings leading to one chamber. Complex burrow systems have one or more surface openings leading to multiple chambers (Newman, 1987; Markwell, 1997). The entrances of the fairy prion burrows are generally narrow becoming wider deeper in the tunnel eventually opening to a chamber. Burrow length ranges from 20–200 cm, averaging 76 cm. Burrows usually have a curve to block sunlight from the nesting chamber, and shorter burrows (20–30 cm) often have a sharp bend in the tunnel (Markwell, 1997).

Squamata—Amphisbeanians

Extant amphisbeanian.—Amphisbeanians are primarily limbless with an elongate body, cylindrical head and trunk (Gans, 1969, Hembree and Hasiotis, 2006). Amphisbeanians are well suited for a fossorial lifestyle because the skulls of several species are compressed to become horizontally flattened and shovel-like or vertically flattened and keel-like (Gans, 1974, 1978). Amphisbeanians with horizontally flattened heads are able to excavate burrows by using the horizontal edge to first penetrate the soil, and then widen the tunnel by raising the head and compressing the soil against the soil onto the root and further smoothing it out with its body (Gans, 1969, 1974; Wake, 1993).

Neoichnological experiments with the amphisbeanian allowed Hembree and Hasiotis (2006) to document in detail the burrow morphologies. Amphisbeanians excavated burrows in 10-gallon aquariums, and multiple experiments were used changing the medium composition soil moisture to document changes in morphologies (Hembree and Hasiotis, 2006). Burrow morphologies discussed here represent the experiment in a loose, but cohesive medium . Morphologies were documented in two (2D) and three dimensions (3D). An amphisbeanian burrow comprises a three-dimensional network of complex interconnected tunnels, with individual tunnels horizontal to vertical in orientation and straight to sinuous, cylindrical in shape, with dimensions from 1.5–2.5 cm. The most common morphology was an S-shaped tunnel with secondary morphologies consisting of short, straight or curved tunnels that branch often. The branching was variable but was commonly between 30° and 90°. No terminal chambers were found in the burrow network. The burrow walls were generally smooth (Fig. 37).

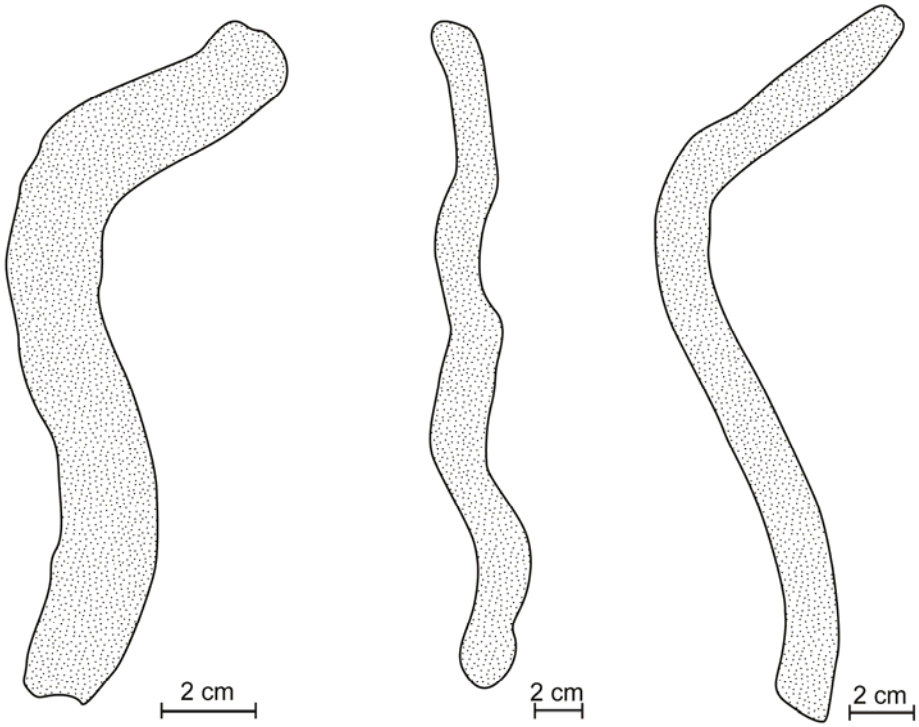

FIGURE 37—Architecture of fossil amphisbeanian burrows.

Few morphological changes of the burrows occurred owing to changes in media composition. In clay-rich soils in 3D casts there were triangular impressions on the burrow walls, but tunnels are smooth and flat on the bottom. These triangular impressions were created from the triangular snout of the amphisbeanian pushing the sediment into the sides and roof of the tunnels. Burrows excavated in the clay-poor soil showed a significant difference in the preservation of the burrows owing to the collapse of the tunnels. The burrows described in 2D were poorly defined as elongate, sinuous trails of dark, compacted clay and sand, and they did not show the complex network of interconnected burrows. The burrows produced within the alternating layers of clay-poor and clay-sand soil in 2D exposures show evidence of sediment mixing, open burrows in the clay-sand soil lined with clay, and collapsed burrows in the clay-

poor soils visible. The collapsed tunnels are visible because of clay linings. These morphologies seen in particular layers are similar to the other experiments with the respective media conditions.

Few morphological changes occurred owing to differences in the soil moisture. The more sandy soils with higher moisture levels resulted in the preservation of more open interconnected tunnels, differing from the lower moisture levels that allowed burrows to collapse easier. Burrows in the clay-rich soils that represented greater moisture levels often showed morphological differences owing to deformation by shrinking of the wet tunnels that caused tunnels to be narrower and flatter.

Fossil amphisbeanian.—Potential amphisbeanian burrows are described from the Eocene Willwood Formation of Central Wyoming and the Miocene Pawnee Creek Formation of northeastern Colorado, however, they are not found with any amphisbeanian body fossils (Hembree and Hasiotis, 2006). The burrows in the Willwood Formation occur in paleosols as individual, isolated burrow casts, with circular to ovoid cross sections, sinuous morphologies, and sometimes tapering to an asymmetrical point. The dimensions of the burrows are 1.0–1.5 cm in diameter and 15–40 cm in length. The burrows are interpreted to be part of an incomplete network because of the absence of branching along with irregular terminations.

The burrows found in the Pawnee Creek Formation represent a more complete burrow network that comprises complex branching networks in a boxwork of elongate, sinuous horizontal tunnels, and short, curved horizontal and subvertical tunnels in a paleosol. These burrows are assigned to the ichnotaxon *Kladosystemites homocylindrichnus* (Hembree and Hasiotis, 2008). These networks extend up to 1 m laterally in outcrop, and 20 cm deep. Individual burrow casts are cylindrical in morphology with a circular to elliptical cross section

and 1.5–3.0 cm in diameter. Tunnels ranged from straight to sinuous that can form U- and S-shaped patterns, with multiple branching points (Hembree and Hasiotis, 2006).

Squamata—Lacertilia

Extant Lacertilia.—Lacertilia represent many of the common lizards, including iguanas and geckos. Twenty-six burrows near water courses were described and measured of the monitor lizard *Varanus mertensi* (Mayes, 2007). The burrows are simple in architecture with all but one having one entrance. No branching was documented and the tunnels lead to a single terminal chamber. Nineteen burrows are straight with an upward slope, five curved with an upward slope, and two followed the shape of the cracks within rock crevices. Burrows ranged from 30–248 cm long with an average of 131.4 cm. All the burrows, except for the ones in rock crevices, had a flat bottom and arched roof at the burrow entrance. The entrance width and height range from 5–25 cm and 5–20 cm respectively, with an average of 15.5 cm wide and 9.7 cm high.

Varanus bengalensis is known to occupy abandoned rodent burrows and rock crevices, but also often excavates their own burrows in high sandy bunds surrounding agricultural plots on terraces and within termitaria (Auffenberg, 1983). These burrows of *V. bengalensis* comprise simple tunnels with oval cross sections with a more convex roof then the floor. Tunnel openings are generally wider than the rest of the tunnel, and further in the tunnel the cross section becomes more cylindrical (Fig. 38A–C). Burrows often had 1–2 cm of loose earth accumulated towards the terminal end (Auffenberg, 1983) (Fig. 38A). The average burrow length is 1.02 m, and burrow depth ranges from 51–121 cm. Tunnels of other animal burrows often connected to the *V. bengalensis* burrows (Auffenberg, 1983). Several burrows of *V. bengalensis* occur in each abandoned termitaria. Each termitaria had several openings ranging from 1–16, averaging 6.6.

Several *V. bengalensis* are seen running into the same burrow; however, the burrows rarely connected underground. Burrow lengths and widths are more variable then those excavated in the sand bunds. The burrow lengths range from 78–121 cm and 87–140 cm in depth. Many other animals also use the termitaria as refuge areas (Auffenberg, 1983).

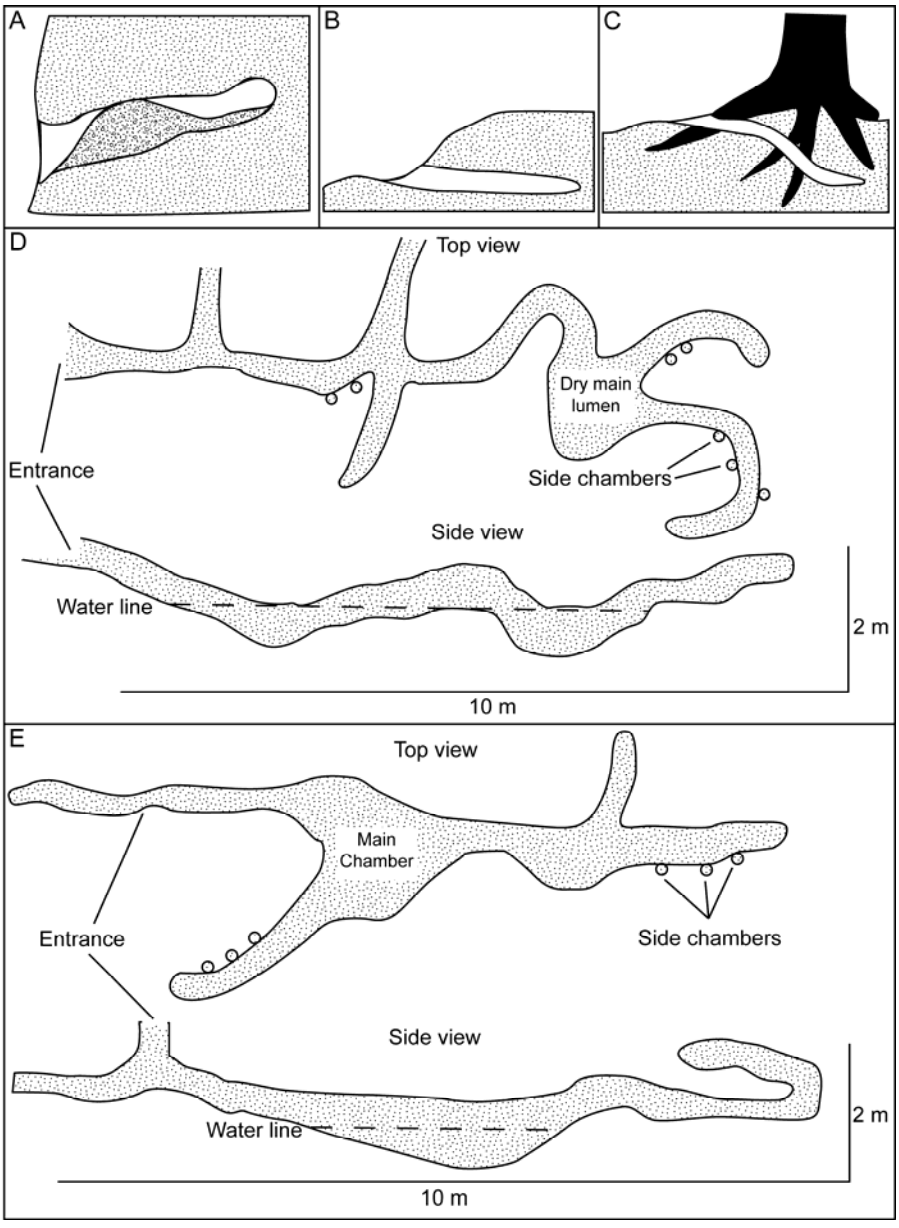

FIGURE 38—Architecture of monitor lizard burrows. A). *Varanus bengalensis* burrow in a vertical bank. Note loose sediment piled up in the tunnel. B). Typical longitudinal profile of a *V. bengalensis* burrow. C). Typical longitudinal profile of a *V. bengalensis* burrow with obstructions in subsurface. Modified from Auffenberg (1983). D–E). Top and side view of two *Varanus salvator* burrows. Modified from Traeholt (1995).

Burrows of *Varanus salvator*, *V. komodoensis*, and *V. griseus* are more complex with more branching and chambers (Mayes, 2007) (Fig. 38D–E). Two burrows of *V. salvator* occur in a riverbank, three on level ground, and two on a minor grassy slope (Traeholt, 1995). These burrows are normally excavated and used by multiple individuals, but often a single individual uses them for prolonged periods. The burrows generally have a single opening; however, two have two openings, and all have an oval cross section, with the roof more curved then the floor. The size of the entrances varies from 40 x 42 cm to 75 x 67 cm and decrease in size to became more cylindrical further inside the burrow. The angle of inclination of the burrows average 4.8°. The beginning of burrows always sloped downward then upward creating a low point where water often collected. After the burrow began to slope upward again, the tunnels lead to an enlarged chamber that had multiple branches coming off. The number of branches in a burrow varied between 4 and 7. The branches are ~50% smaller than the entrance tunnel. The number of side chambers in two burrows systems considered nesting sites was estimated to be 8 and 9. The longest part of a burrow system varies from 3.2–14.3 m and average 9.5 m.

Norris (1953) investigated burrows of the desert iguana *Dipsosaurus dorsalis*. These iguanas are often found occupying abandoned mammal burrows in the northern Sonora of Mexico. Burrows are simple with one entrance and a tunnel a 45.7 cm long extending 15.2 cm

deep into the soil, or complex with multiple entrances with tunnels 91.4–122 cm long and extending up to 61 cm below the surface (Fig. 39A). *Dipsosaurus* will excavate burrows when abandoned mammal burrows are not available. *Dipsosaurus*-excavated burrows are generally simple in architecture, but consist of three tunnels to the surface ~3.8 cm wide, two of which are plugged. A chamber is found ~6.3 cm below the surface, and is oval in shape and 8.9 cm long. Juvenile burrows tend to be smaller and shallower. Two of these burrows comprise small tunnels that are ~30.4 cm long and extend 3.8 cm deep. Two entrances, one of which was blocked, connect these tunnels. No chamber is present in the juvenile burrows.

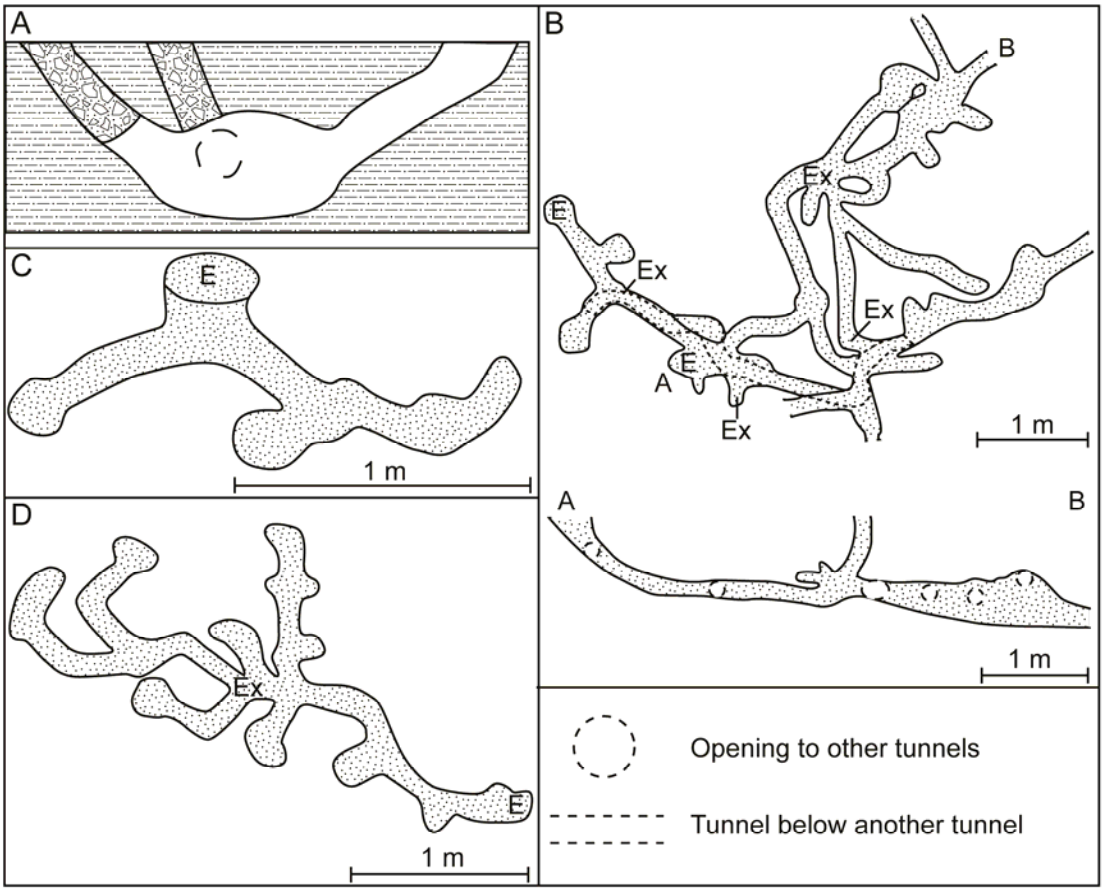

FIGURE 39—Burrows of iguanas. A). Typical morphology of a Dipsosaurus burrow. Modified from Norris (1953). B). Morphology of a complex multiseason *Iguana iguana* burrow from a top

view. Side view is a cross section from A to B. C). Morphology of a single season simple *I. iguana* burrow. D). Morphology of a multiseason simple *I. iguana* burrow. Modified from Rand and Dugan (1983). E = Entrance to tunnel, Ex = Exit to surface from tunnels.

Burrows of the black iguana *Ctenosaura similis* where studied at Palo Verde, Costa Rica (Burger and Gochfeld, 1991). The black iguanas excavate burrows most often in banks, but also use existing burrows in logs, roots, trees, rocks, and boulders. Burger and Gochfeld, (1991) investigated 178 burrows and found that burrows are generally wider then high with an average 16.3 cm wide and 10.8 cm high. The average depths of the burrows are 79.9 cm.

Burrows occupied by nesting females of *Iguana iguana* (Fig. 39B–D) at two localities in Panama are found to change in complexity if used for multiple seasons (Rand and Dugan, 1983). Several solitary burrows are also described on the Barro Colorado Island laboratory clearing. Observations of females digging show that the burrows begin as an entrance pit about 20 cm deep with a tunnel ~10–15 cm in diameter later excavated. At the beginning of the egg-laying season a female will exit through the same hole she entered when spent, and fill it with sediment. Later in the season if another female occupies that entrance, the other female underground will excavate a different exit hole that is a shaft 20–40 cm long.

Solitary burrows comprise one entrance leading to a curving tunnel that ends in a terminal chamber. Burrows are 50–100 cm long and nesting chambers are 30–40 cm deep. In another locality where the soil was hard, burrows are only ~30 cm long with terminal chambers 15–20 cm below the surface.

Communal burrows of the iguana comprise single season and multiple season uses. The single season burrows comprise an entrance hole from which two main tunnels led in different

directions. Along the main tunnels, many short, side branches lead to nest chambers (Fig. 39C). The chambers, side tunnels, and most of the main tunnels are infilled with earth except for an exit hole at one locality. Multiseason burrows are much more complicated then the single season burrows (Figs 39B, D). Tunnels in the complex burrow systems are longer, and branch more often; in one particular system tunnels joined back together. Tunnels also are deeper, passed under one another, and had several entrances to the surface; one system had several exit holes. Complex burrow systems have more chambers, and they are larger and deeper than the simple burrows chambers.

Summary

Ancient and extant reptile burrows are both simple and complex in architecture. Turtles, crocodiles, sphedondonts, and monitor lizards tend to construct large diameter, long, simple tunnels that have may curve a few times with one or two branches, but more commonly exhibit no branching. The curve in tunnels is typically because of an obstruction during excavation. Spenodonts and monitor lizards can be found in complex burrow systems that can have multiple openings to the surface, multiple tunnels, and multiple chambers. Spenodonts generally do not excavate their own burrows, but instead occupy bird burrows. Monitor lizards can occupy other animal burrows but they do excavate their own, which exhibit an oval cross section with a roof more curved then the floor. Smaller reptiles, such as the iguanas, create the simplest of complex burrows that can have multiple entrances, tunnels and chambers. The complexity of iguana burrows reflects the number of individuals living together as well as the extent of use. Solitary burrows are the least complex with one entrance with a curving tunnel that leads to a terminal chamber. Communal burrows are more complex, but the single season burrows are less complex

then the multiple season burrows. Modern and ancient amphisbeanian burrows are the most complex and comprise a three-dimensional network of complex interconnected tunnels, with individual tunnels horizontal to vertical in orientation, cylindrical in shape that are straight to sinuous.

THERAPSID BURROWS

Therapsids are a group of synapsids that existed from Upper Permian to Middle Jurassic (Carroll, 1988). Multiple burrows of therapsids have been discovered in South Africa and Antarctica (Smith, 1987; Groenewald et al., 2001; Damiani et al., 2003). The significance of finding evidence of burrowing in these basal synapsids is that it shows burrowing was common among synapsids and had strong adaptive value in the evolution of mammals (Damiani et al., 2003).

Burrow casts the therapsid *Diictodon* were discovered from the Permian in the Beaufort Group of the Karoo Basin in South Africa based on articulated skeletons (Smith, 1987). The burrows are preserved in siltstones from a proximal floodplain and are infilled by fine-grained sandstone and siltstones. Approximately 50 *in-situ* burrows are described that are helical in architecture and consist of a shaft spiraling vertically through 2 to 3 whorls to a terminal chamber (Fig. 40). Shaft diameters consistently increase from 6 cm at the entrance to 25 cm at the terminal chamber which straightens and widens. The cross sectional view of the burrows at the entry and first whorl are plano-convex, the second whorl is more elliptical, and the terminal chamber has a flatted bi-convex cross section. The ramp angle of whorls ranged from 10 to 32 degrees. The walls of the shaft and terminal chambers consist of claw marks and snout marks made from *Diictodon* owing to the excavation of the burrow. The claw marks appear as parallel

straight to curved ridges, sinuous ridges, and chevron patterns on the shaft walls and terminal chambers.

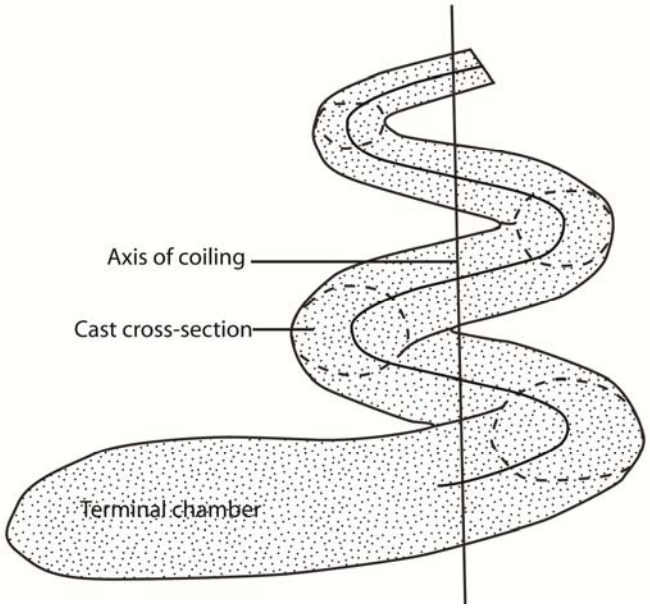

FIGURE 40—Architecture of the therapsid *Diictodon* burrows. Modified from Smith (1987).

The helical burrows represent the oldest evidence of helical architecture in vertebrate burrows, and the first evidence of non-mammalian vertebrate burrows that are helical. Smith (1987) noted that the helical burrows of *Diictodon* are not abundant and are also in a limited stratigraphic range to represent a structure for normal dwelling or brooding. Burrows may have been used for hibernation or aestivation in extreme climatic conditions.

Complex burrows excavated from the therapsid *Trirachodon* were discovered in the Lower Triassic Driekoppen Formation of South Africa and represent the oldest evidence of colonial dwelling in tetrapods (Groenewald et al., 2001). Twenty nearly complete skeletons of *Trirachodon* individuals were found near the burrows. The burrow systems occur within a proximal flood plain and overbank complex that was adjacent to a channel (Fig. 41A). The

tunnel near the entrance showed the greatest dimensions at 16 cm entering the media at an angle of approximately 8° and curves as it descends. The cross sectional view of the entrance tunnel was 15.4 cm wide and 6.4 cm high giving it a shape of an ellipse but with a bilobate morphology on the floor that gave it an appearance of an upside down U shape (Fig. 41B). Multiple side branches came off the main tunnel with similar morphologies to the main tunnel. Increasing in depth, the diameter of tunnels became smaller ranging from 5–12 cm wide, the curvatures stronger, and the complexity greater with tunnels creating a right angle junction. At the end of burrow systems the tunnels began to taper until the tunnels become strongly flattened and end in wedge shaped terminal chamber. Overall the shafts and tunnels showed a variation in inclination from 1–23°. Scratch marks are observed on the bases, sides, and upper margins of the burrows occurring as diagonal and transverse marks.

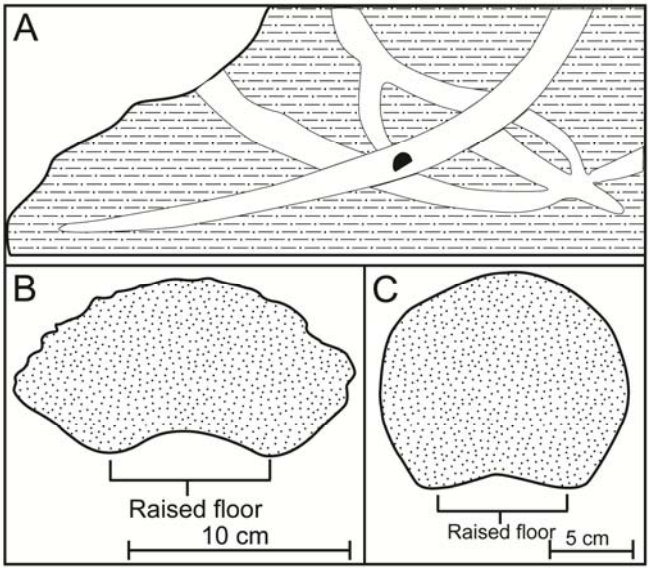

FIGURE 41—Architecture of therapsid burrows. A). Reconstruction of a *Trirachodon* burrow system. B). Bilobate morphology of a *Trirachodon* burrow cast. Modified from Groenewald et al. (2001). C). Bilobate morphology a *Thrinaxodon* burrow cast. Modified from Damiani et al. (2003).

The earliest evidence of a cynodont synapsid burrowing comes from a partial burrow cast containing an articulated skeleton of *Thrinaxodon liorhinus* in the Karoo Basin of South Africa (Damiani et al., 2003). The burrow casts were found in floodplain deposits adjacent to a river. The burrow casts were filled in by fine-grained sandstone owing to the river flooding its banks. The partial burrow is represented by the terminal chamber based on its expanded and rounded edge. The skeleton of the *Thrinaxodon* is found in the terminal chamber curled up. The edge of the cast has been broken cleanly and shows a nice outline of the tunnel that lead to the terminal chamber. The cross section is similar to the burrow cast described by Groenewald et al. (2001) in that it has a rounded outline, but on the floor it has a well developed bilobate morphology giving it the appearance of an upside down U shape (Fig. 41C). Based on the size of the *Thrinaxodon* and the width of the burrow, only one individual would fit in the shaft at a time. This differs from interpretation of Groenewald et al. (2001) who saw the therapsids moving on either side of the raised floor because their skeletons are too small to occupy the entire burrow themselves. Scratch marks are seen on the surfaces of the burrow cast as parallel ridges. Other surficial features shown the surface of the burrow casts include invertebrate bioturbation that was preserved as a rod-like morphology (Damiani et al., 2003).

Complex burrows in the Owl Rock Member of the Triassic Chinle Formation comprises short, small diameter tunnels that interconnect to larger diameter tunnels, shafts, and spiral shafts with chambers (Hasiotis et al., 2004). The cross sections of the burrows are circular to subcircular with dimensions ranging from 4–15 cm. The surficial morphology of the burrows comprises bumpy and irregular surfaces and scratch marks.

Two types of burrows were found in the Lower Triassic Fremouw Formation of Antarctica within floodplain deposits (Miller et al., 2001). One of the burrows, designated type G

burrows appear to be quite simple in architecture comprising subhorizontal to gently inclined, straight to slightly curved tunnels. The burrows have an elliptical cross section with diameters ranging from 8–19 cm and extending 2–50 cm. Some of the tunnels increased in diameter extending downward, and one specimen may have been helical. There was no lining observed on the burrow walls, but the surficial morphology of the burrows comprises scratch marks oriented tangentially or longitudinally to the burrow axis.

Type L burrows are gently inclined to subhorizontal with tunnels steeply inclined near the top of the burrow, and become gently inclined downward (Miller et al., 2001). Two specimens are also J-shaped and some slightly curve in plan view. Branching is rare, but occurs both in horizontal and vertical planes mostly at low angles. One specimen branched at a high angle in the vertical plane. The cross sectional shape of the burrows is nearly circular to elliptical with dimensions ranging from 2–6.5 cm, averaging 3.9 cm. The burrows have a groove on the bottom surface ~1 cm deep that creates a raised floor. The surficial morphology of the burrows comprises bumpy irregular surfaces and scratch marks oriented longitudinally, tangential, and rarely transverse to the long axis. Miller et al. (2001) had difficulties determining the origin of the Type L burrows between crayfish and tetrapods, but Hasiotis et al. (2004) attributes these burrows to being constructed by therapsids because of the lack of key burrow characteristics in type L burrows that occur in ancient and extant crayfish burrows.

Two burrows occur in the interdune deposits of the Lower Jurassic Navajo Sandstone (Fig. 42). These burrows are assigned to the ichnotaxa *Schemalitus psalihyponomes*. *S. psalihyponomes* is a dorsoventrally flattened tunnel; two specimens have dimensions of 35 cm wide, 18 cm high, and 58 cm wide, 18 cm high. The best-preserved example of *S. psalihyponomes* is ~6.17 m long and extends from the sandstone into the underlying mudstone at

~25° (Fig. 42A). The portion of *S. psalihyponomes* in sandstone is poorly preserved for ~4 m as a weathered ledge with mud rip-up clasts delineating the base of the tunnel. The portion of *S. psalihyponomes* in mudstone is well preserved for ~2.2 m and curves into the mudstone until it extends into the outcrop out of view. *S. psalihyponomes* exhibits a bilobate morphology in the mudstone created from a raised floor. The raised floor is 20–25 cm wide, measured from the center of each lobe, and 2–2.5 cm deep, measured from the base of the lobe to the high of the raised floor. The lobe width is ~15–20 cm for both sides exposed in the mudstone. The second structure of *S. psalihyponomes* is seen in cross-section in the mudstone (Fig. 42B). This structure has massive fill with mud rip-up clasts on the perimeter of the structure.

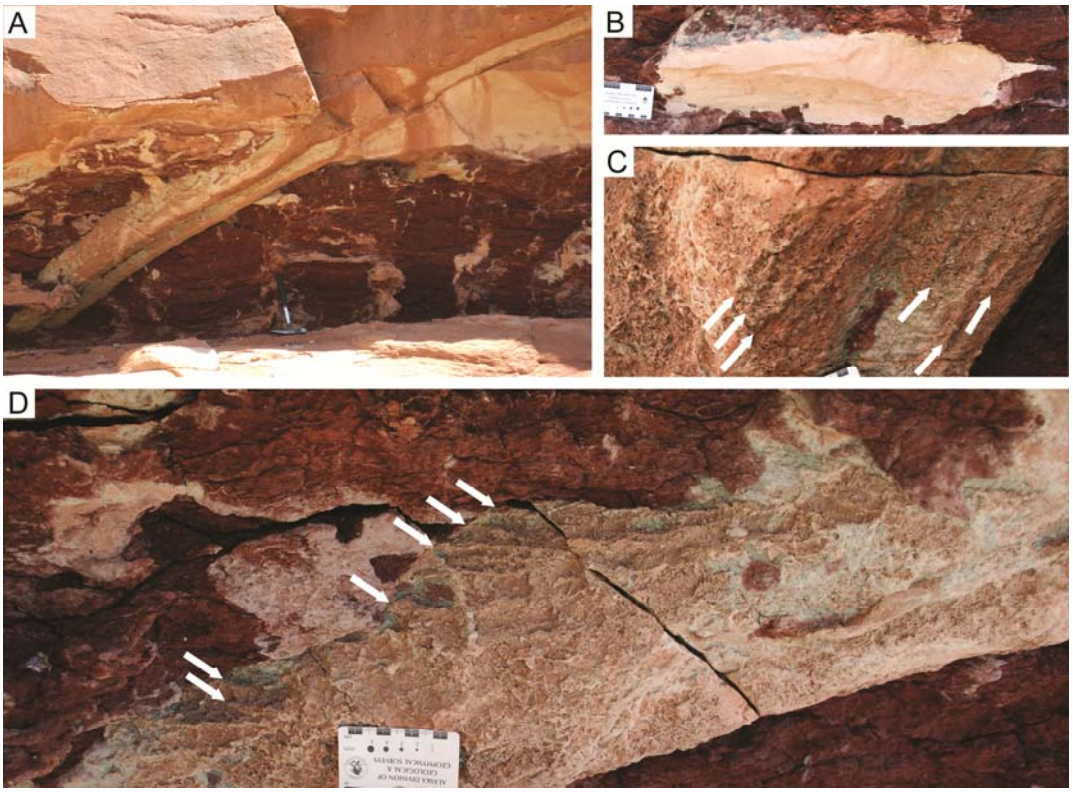

FIGURE 42—Burrows in the Navajo Sandstone assigned to the ichnotaxa *Schemalitus psalihyponomes*.

Surficial morphologies of *S. psalihyponomes* include sets of two or three scratch marks extending from the upper part of the wall and along the lobes of the structure (Fig. 42C, D). Scratch marks range from 4.0 to 8.0 mm wide (average 5 mm) and 2.5 to 20 cm long (average 8.8 cm); distances between individual marks range from 1.5 to 3 cm (average 2.3 cm). Scratch marks from the upper part of the wall of *S. psalihyponomes* are inclined at angles ranging from 14 to 30° (average 23.2°). Scratch marks on the base of the lobe range from 6 to 11 mm wide (average 9 mm) and 3 to 18.5 cm long (average 9.8 cm); distances between individual marks range from 1.3 to 3.5 cm (average 2.6 cm). Scratch marks converge towards the midline at <10°, however, one scratch mark crosscuts others at a 30° angle.

Five large burrow casts are found in fluvial deposits of the Upper Triassic fluvial deposits of the Holy Cross Mountains in central Poland are thought to have been excavated by cynodonts (Talanda et al., 2011) (Fig. 43) . The burrows occur in a red mudstone and are infilled by a green siltsone. All the burrows are similar in morphology consisting of long tunnels inclined 18–36° from horizontal that end in terminal chambers. The burrows range in length from 1–3.75 m. The cross sectional shapes of the tunnels are strongly elliptical with the floors and ceiling of the burrows being relatively flat with the heights of the burrows that range from 7–9 cm. The burrows widen laterally toward the entrance. In larger burrows chambers are 30-40 cm long and are higher then the burrows tunnels, whereas terminal chambers in smaller burrows are difficult to distinguish. The burrows walls are relatively smooth, however Talanda et al. (2011) note that the preservational mode is not ideal to preserve these features.

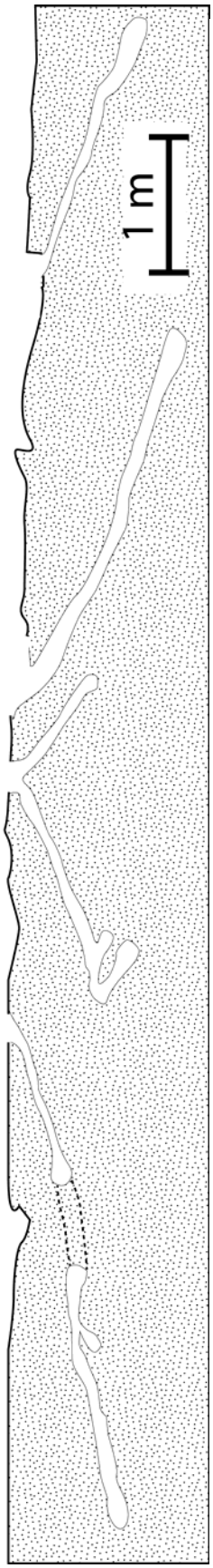

Figure 43—Cross sectional view of large subhorizontal burrows found within fluvial deposits in Poland.

Summary of therapsid burrows

Morphologies of therapsid burrows vary in complexity. Morphology of simple burrows comprises long, inclined curving tunnels that rarely branch. Many burrows have a raised floor that creates a bilobate morphology. Scratch marks are normally seen on the burrow walls. Complexity of burrows increased with those that have a helical architecture. Complexity of burrows further increased with those that branch, and with tunnels and shafts of sinuous and helical architecture that lead to larger tunnels and chambers. Scratch marks as well as beak marks are normally seen on the burrow walls and also on those of the terminal chambers. The morphologies of the therapsid burrows are similar to those of reptiles, especially those of crocodiles and turtles, but there may be some ways to help discern between them if body fossils are not found. Therapsid burrows will only be found in sediments from the Permian until the Middle Jurassic. Modern crocodiles normally excavate burrows into banks near rivers and otherwise near water areas, so fossil crocodile burrows may be found in areas that appeared to be inundated with water. Modern turtle burrows normally have a cross sectional shape that is hemispheric because of the turtle's carapace, so a fossil turtle burrow may likely show the same cross sectional shapes.

MAMMAL BURROWS

The class mammalia evolved ~220 million years ago and diversified into multiple lineages, of which ~82 percent of all families within mammalia contain burrowers (Voorhies et al., 1975; Jaworowska et al., 2004). The orders Marsupialia, Insectivores, and Rodentia have some members that live a complete subterranean lifestyle (Reichman and Smith, 1990).

Carnivora

Exant carnivora.—Aardwolfs are a nocturnal termite eating organism that lives in semi-arid environments of southern Africa (Anderson and Richardson, 2005). During the day the aardwolf stays in a den, however, the aardwolf is not specialized for digging, so instead modify the burrows of springhares. The number of aardwolf dens investigated was 42. The aardwolf dens are simple in architecture predominately have one entrance, with rarely two entrances (Fig. 44). The tunnels do not branch and do not have a chamber. The cross sectional shapes of the burrows are semi-circular with the width greater than the height. The den entrances are larger than the rest of the tunnels and averaged 38 cm wide and 25.5 cm high, and have a depth of 49.6 cm. The inclination of the burrows was ~19°. Two aardwolf dens that were measured internally have a tunnel width of 34.8 cm and 36.8 cm, tunnel height of 20.7 cm and 21.7 cm, and tunnel lengths of 6.5 and 5.1 m respectively. A burrow fill was only noticed when active digging of the burrows by humans was done, and the aardwolfs were seen infilling the burrow likely for protection. At the end of the aardwolf tunnel the burrows narrowed into smaller burrows that were likely the original springhare burrows.

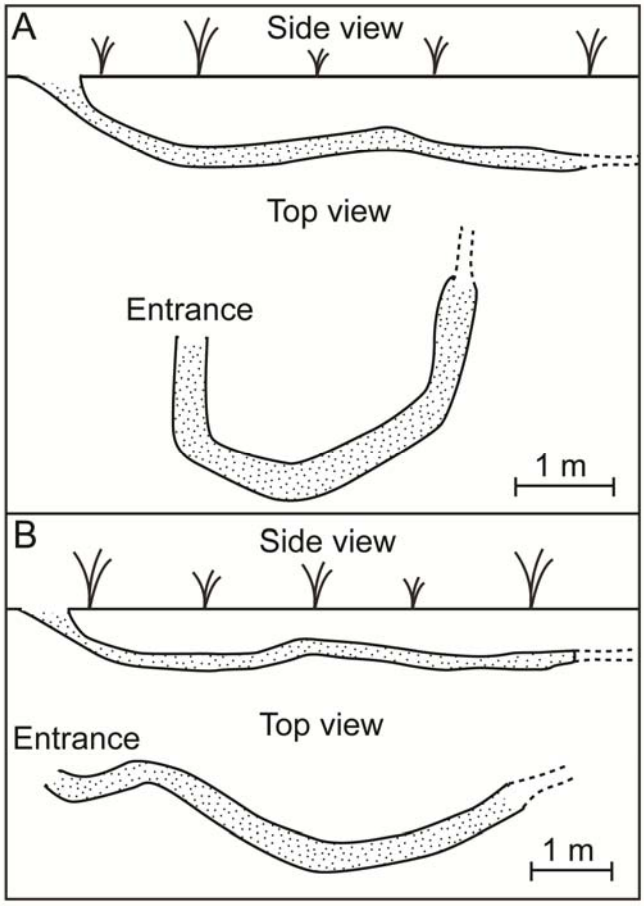

FIGURE 44—Side and top view of Aardwolf burrows. Dotted line represents beginning of springhare burrows not modified by aardwolfs. Modified from Anderson and Richardson (2005).

Fossil carnivora.—Three dens containing partial skeletons of bear dogs, canids, and mustelids are found in Agate Fossil Beds National Monument, Nebraska (Hunt et al., 1983) (Fig. 45). Den 1 contains a burrow that is that is slightly inclined, and another burrow has a nearly vertical entrance both with tunnels that lead down about 1 m to a pit likely the main den chamber. The internal burrow diameters for the first burrow ranges from 15–46 cm and the second burrow ranges from 30–66 cm. The second den contains a burrow that has an inclination

of 15cm/m, is 2 m long, and has a maximum diameter ranging from 80–90 cm. The burrow narrows to about 40 cm and ends in a terminal lobe ~50 cm wide. The third den contains a burrow with diameters ranging 30–55 cm, and it is unclear if it connects to an area where a partial skeleton of a bear dog is located in a burrow fill. The burrows are thought to have been mainly constructed or remodeled by bear dogs because of the large size and form of the burrows similar to large canids and hyaenids. The several other species found within the burrows are secondary occupants.

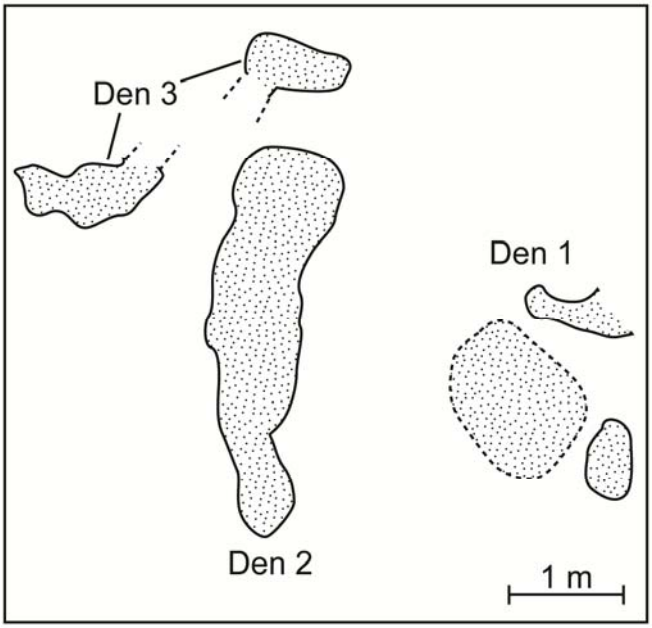

FIGURE 45—Plan map showing orientation of Miocene bear dog burrows to one another. Dotted line represents where a boundary is uncertain. Modified from Hunt et al. (1983).

A burrow from the Miocene Pawnee Creek Formation in Colorado is assigned to the ichotaxa *Katarrhedrites athesphatichnus* (Hembree and Hasiotis, 2008). The burrow entrance is poorly defined, but leads to a 60–70 cm in diameter subhorizontal tunnel inclined 15–20°. With increasing depth the tunnel decreases in inclination to 1–5° and also widens to a terminal

chamber 80–85 cm in diameter. The total length of the tunnel is 1.85 m and reaches a maximum depth of 1–1.1 m. The burrows did not preserve any surficial markings.

A helical burrow from the Miocene Pawnee Creek Formation is assigned to the ichnotaxa *Daimonelix petalichnus* (Hembree and Hasiotis, 2008) (Fig. 46). The burrow has an amorphous and enlarged upper portion, and may have had a surface mound. The burrow is vertically oriented, helical in architecture with three to five coils that are 30–50 cm in diameter loosely coiled around a central axis, and ends in a single enlarged terminal chamber. Tunnels are inclined 5–30° becoming less inclined with each successive coil. The helical burrows extend laterally 1–1.5 m and extend to a depth of 2–3 m, and with lengths of 0.75–1.5 m.

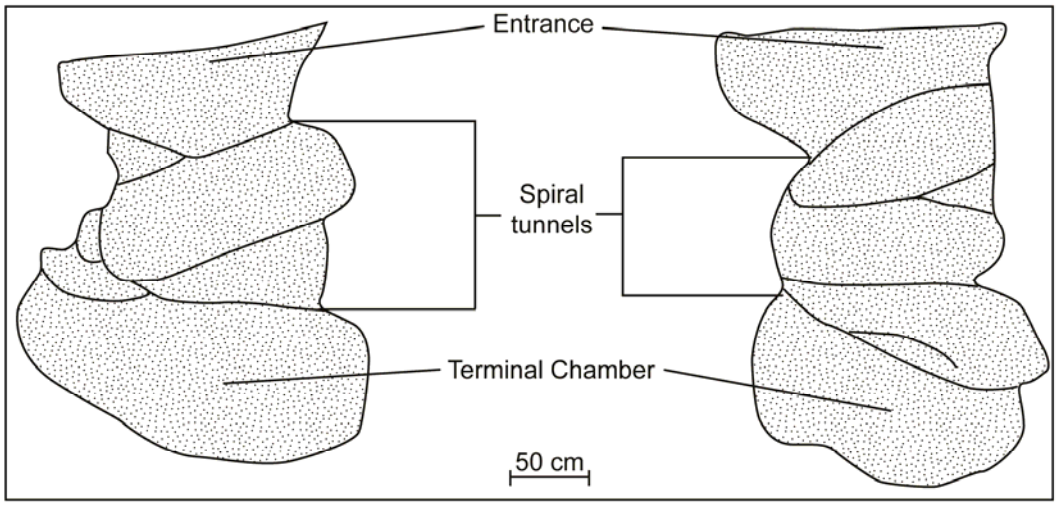

FIGURE 46—Burrows of *Daimonelix petalichnus* from the Pawnee Creek Formation, Colorado. Modified from Hembree and Hasiotis (2008).

Rodentia

Extant rodent.— Rodentia is an order of mammals that includes mice, rats, beavers, voles, and many more animals that have two continuously growing incisors in the upper and lower jaws. Rodent burrows tend to excavate the most elaborate burrow systems, and depending

on the species use them for a variety of reasons including shelter, food storage, and foraging (Reichman and Smith, 1990).

Microtus ochrogaster, also known as prairie voles, have nesting burrows as either male-female pairs, or as communal, social groups (Mankin and Getz, 1994). The complexities of the nesting burrows differ owing to the different lifestyles of the voles (Fig. 47). Other burrows are found that contained no nesting chamber and they are thought to be those of hiding or escape burrows but are not described. Escape burrow showed the same morphology and dimensions of the nesting burrows. The typical nesting burrow comprises interconnecting tunnels with an average of six entrance holes, ranging from 2–17. Sixteen of the 24 burrows described had one nest chamber, and the other had two. Tunnels did not always connect to one another, and some also ended abruptly underground. The tunnels and nesting chamber tended to occur on the same plane. The burrow characteristics in both male-female pairs and communal burrows that are consistent include the diameter of the tunnel (4.7 cm), the number of nest chambers (~1.3), and the distance from the surface to the floor of the nest chamber (~15 cm).

Comparisons between the male-female and the communal group show that the communal burrows are larger and more complex (Fig. 47A). The total length of the burrows are 80% longer, increasing from 92.8 cm in the male-female pair to 117 cm in the communal burrows, and the total width increased from 51.3 cm to 77 cm while also doubling the number of surface entrances. The volume of the nest chambers for communal burrows was 49% larger then male-female pair increasing from 1336 cm^3 to 1991 cm^3.

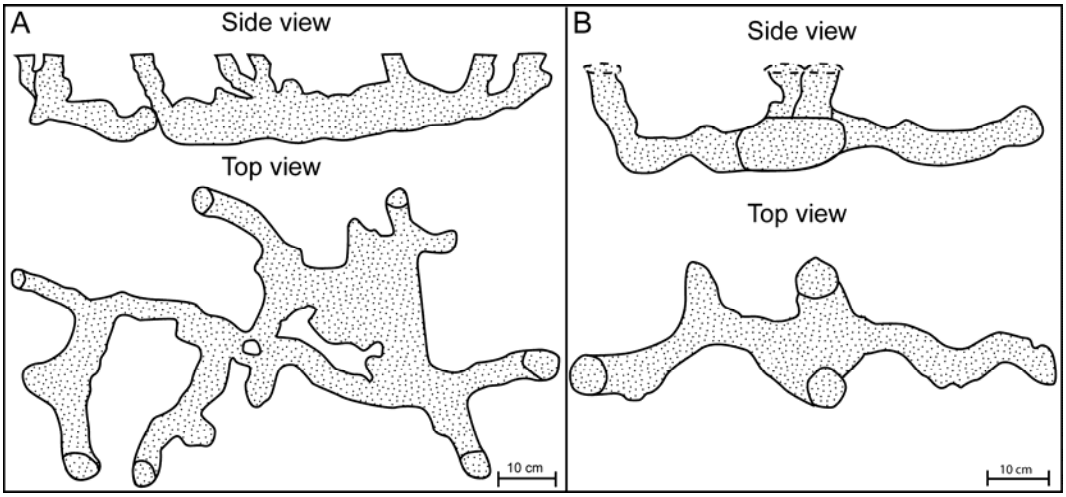

FIGURE 47—Top and side views of *Microtus ochrogaster* burrows. A). Communal burrow system. B). Male-female pair.

Burrow characteristics are also documented for the male-female pair between the winter and summer seasons. The number of average entrance holes decreased from 6.3 to 4.3, total length decreased 102.8 cm to 86.8 cm, total width decreased 55.1 to 49.1, length of tunnel decreased 264.3 cm to 147.9 cm, and volume of nest chambers decreased from1585 cm^3 to 1129 cm^3 from the winter to the summer season. The diameter of tunnels (~4.8) and number of nest chambers (~1.3) did not change much. The distance from the surface to the ceiling and the floor of the nest chamber was shallower in the summer being 4.6 cm and 14.1 cm respectively, compared to the winters 7.3 cm and 16.4 cm respectively.

Spalacopus cyanus is a rodent found in Chile, and is shown to excavate long complex burrow systems different than other rodents (Begall and Gallardo, 2000). Multiple individuals lived within the same burrow complex. On one side of the entrance an oval mound was commonly found that was ~29 x 33 x 11 cm. Tunnels comprise a complex network of interconnected tunnels that lacks a straight main tunnel (Fig. 48). The total length of the burrow

is estimated to be ~600 m, and the depth of the burrow is ~15 cm. The tunnels openings are unplugged. The tunnels have an average diameter of 6 cm and the length of blind ending tunnels and laterals is ~23 cm. Nests were not found in the two burrow systems excavated carefully, although they were not completely excavated. In four other burrow systems excavated at one locality an average of three nests were found for each system ~30 cm below the surface. The size of the nests vary for each of the burrow systems at the one locality averaging 17.6 cm long, 11.9 cm wide, and 11.1 cm high.

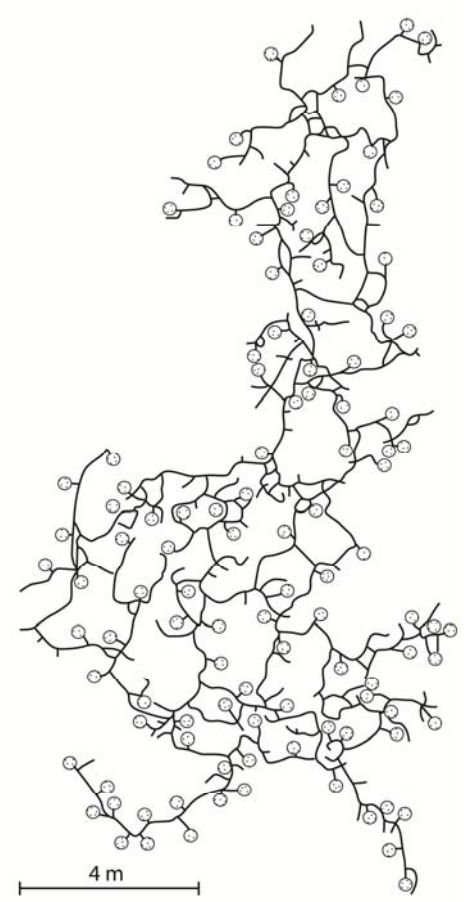

FIGURE 48—Top view of a *Spalacopus cyanus* burrow system. Mounds are represented by circles with dots. Modified from Begall and Gallardo (2000).

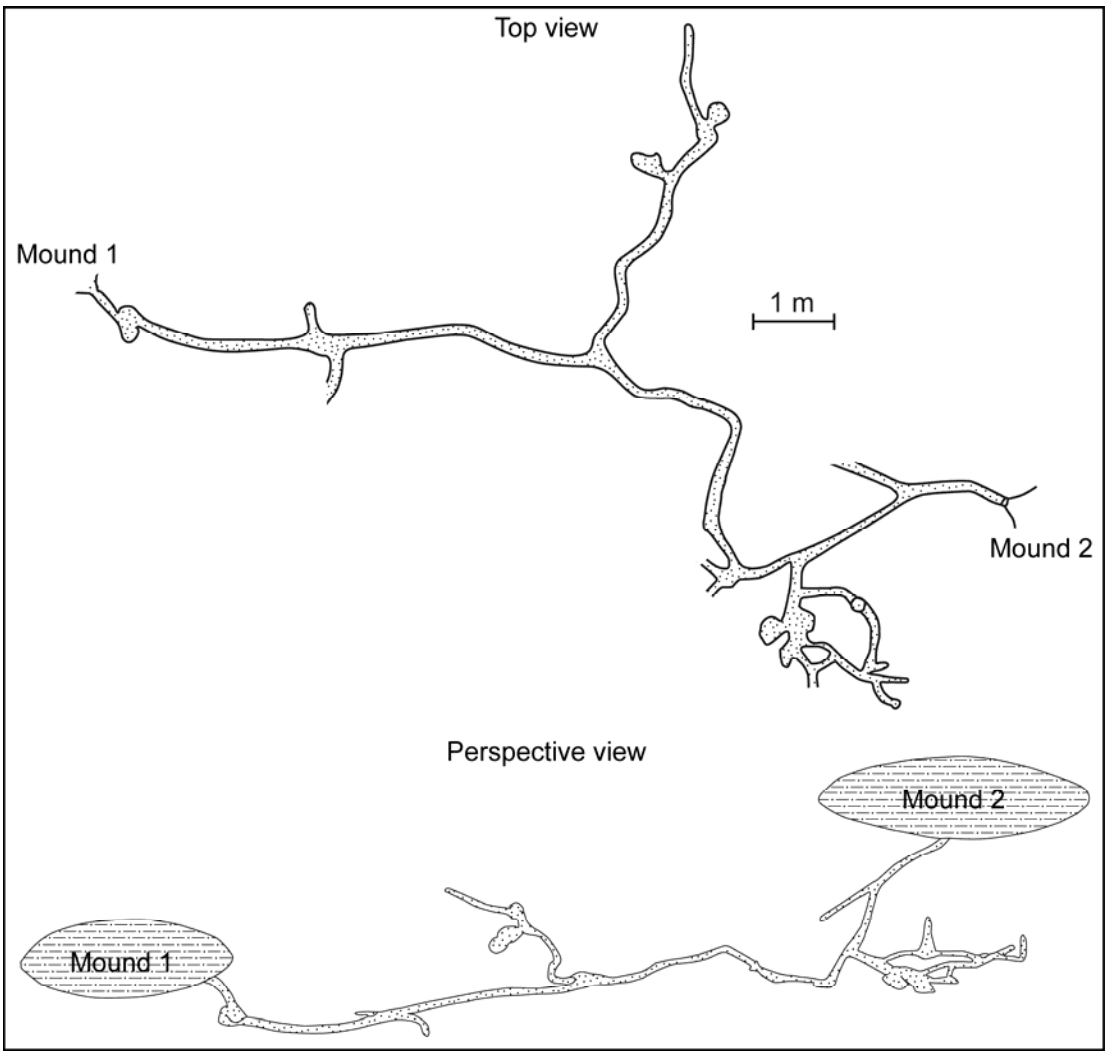

FIGURE 49—Top and perspective view of white-tailed prairie dog burrows. Burrow was not completely excavated. Incompletely excavated tunnels are left open. Modified from Burns et al. (1989).

The morphology of a burrow from the prairie dog *Cynomys leucurus* was excavated and described by Burns et al. (1989) (Fig. 49). The burrow comprises two entrances each with a surface mound that is domed with the one having a diameter of ~2.5 m and the other with a dimension of ~4 x 3.5 m. The tunnel connecting the mounds was ~16.5 m. Approximately 5

lateral tunnels, equaling ~12.8 m off the main tunnel were excavated. The total length of the tunnels was ~29.3 m, and the greatest depth was ~2 m, however, the entire burrow system was not excavated. One area of the burrow systems comprises complex networks of interconnected tunnels. The dimensions of the tunnels are ~10–11 cm. A two part chamber in the burrow system is thought to be a turning bay. Two chambers of globular shape, one with dimensions 24x23 cm high, are thought to represent hibernacula. Three subchambers are also found in the burrow system that may represent maternity areas. The burrow systems also had two vertical termini, one of which was 12 cm in diameter and extended up 39 cm to a blunt end. Many of the tunnels are plugged. The surficial morphology of the burrows comprises paired linear gouges produced from the incisors.

The mole rat includes both solitary and social groups that construct large and complex burrow systems (Fig. 50). Mole rats often construct mounds, often referred to as mole hills, which are composed of soil that is pushed up from the tunnels during construction (e.g. Jarvis and Sale, 1971; Davies and Jarvis, 1986). These mole hills can vary in size, but for the genus *Tachyoryctes* it ranges from 15–40 cm in diameter and 7–15 cm high, and the mole hill of *Heterocephalus* has a diameter of ~35 cm and stands 25–30 cm high (Jarvis and Sale, 1971). The burrows of mole rats often consist of foraging tunnels, bolt holes, and one or more nests. The total lengths of burrows can reach hundreds of meters (e.g., Jarvis and Sale, 1971; Davies and Jarvis, 1986). Foraging tunnels are often simple that branch occasionally. The length of the foraging tunnels can be dependent upon the availability of food. The depth of burrow systems is also important and can change owing to soil horizons, root levels, moisture levels, and temperature gradients (Hickman, 1990). *Tachyoryctes* tunnels run at a depth that was controlled by root, tuber, or rhizome level of the food plants (Jarvis and sale, 1971). Bolt holes are tunnels

that end blindly and are used as quick access tunnels leading to maximum depths so the animal can hide from predators. Many of the burrows are also plugged not only to maintain humidity and temperatures, but also to keep predators out (Hickman, 1990). For a summary of dimensions of architectural features of mole rats see Table 1.

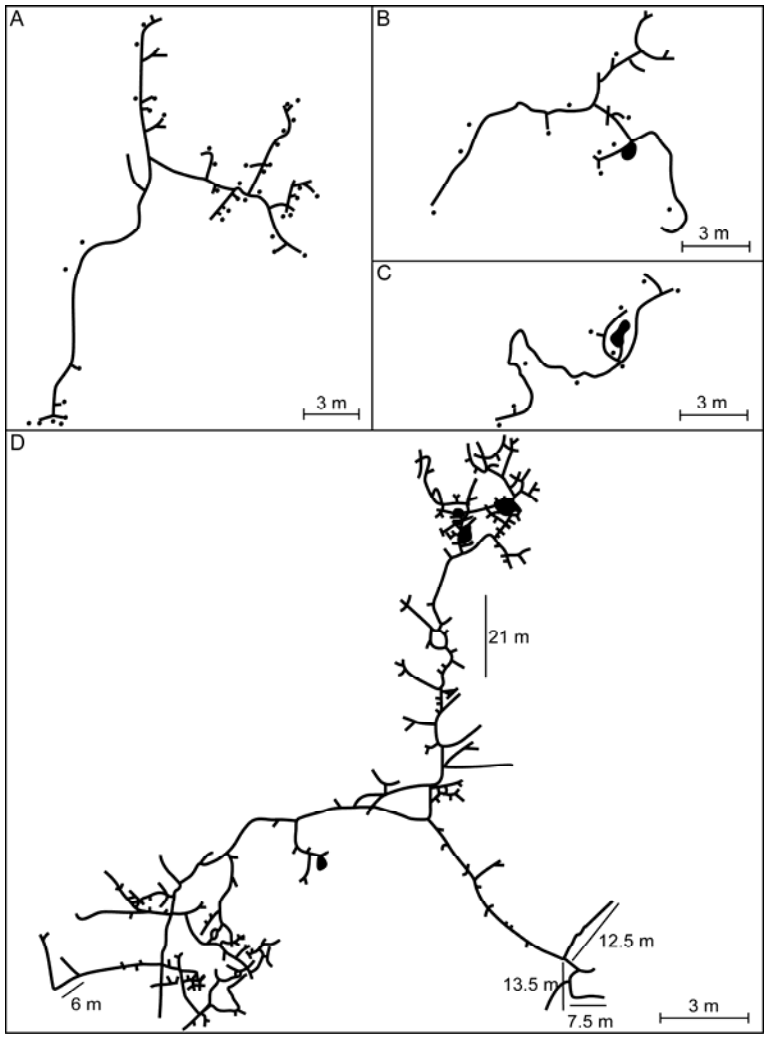

FIGURE 50—Plan view of mole rat burrow systems. A). Burrow of an adult *Heliophobius* female. B). Burrow of an adult *Tachyoryctes* female. C). Burrow of an adult *Tachyoryctes* male. D). Part of a burrow system of *Heterocephalus*. Black dots = mole hills; Larger irregular black areas = nests. Modified from Jarvis and Sale (1971).

TABLE 2—Summary of architectural morphology measurements of mole

Genus	Number of Occupants	Total Length (m)	Shape and Diameter of Foraging Tunnel (cm)	Depth of Foraging Tunnel (cm)	Number of Nests	Shape and Diameter of nests (cm)	Depth of Nests (cm)	Purpose of nests	References
Tachyoryctes	1	14–52	Circular shape; 5–7	19–23	1–2	Spherical, oblong, bottle shape; ~23	30–60	Sleeping	Jarvis and Sale, 1971
Heliophobius	1	47	Circular shape; 5	15–23	1–3	Ciruclar; 8–10	30	Sleeping	Jarvis and Sale, 1971
Heliophobius (Blantyre location)	1	–	Diameter: 5–8 Height: 5.5–8.7	7–20	~3/burrow system	Diameter: 9–25; Height: 10–16; Length: 10–19	7–28	Sleeping	Šumbera et al. (2004)
" "	1	–	–	–	~1.5/burrow system	Diameter: 11–18; Height: 10–14; Length: 14–22	6–17	Food stores	Šumbera et al. (2004)
Heliophobius (Mulanje location)	1	–	Diameter: 6–8.5 Height: 6–8.5	19–30	~3/burrow system	Diameter: 11–17; Height: 10–16; Length: 13–19	21–50	Sleeping	Šumbera et al. (2004)
" "	1	–	–	–	~1.5/burrow system	Diameter: 10–15; Height: 10–15; Length: 14–27	10–53	Food stores	Šumbera et al. (2004)
Heliophobius	1	82–322	5–8.5	7–21	1–8	Width: 6.5–19; Height: 7–25; Length: 9–31	4.5–47	Sleeping	Šumbera et al. (2007)
" "	" "	–	–	–	0–5	Width: 9–24; Height: 8–14; Length: 10–24	9–27	Food caches	Šumbera et al. (2007)
Heterocephalus	30–40	>165	Circular; 3	15–20	5	11–38 x 41	23–45	Sleeping	Jarvis and Sale, 1971
Bathyergus	1	107–420 excludes side branches; greater than 0.4 km with side branches	15–20	40–65	2–6	Avg. Diameter: 17–20 Avg. length: 24–37	40–90	Sleeping/eating	Davies and Jarvis, 1986
" "	" "	–	–	–	1–2	9–17	34–60	Food stores	Davies and Jarvis, 1986
" "	" "	–	–	–	1–7	Diameter: 15–21 Length: 45–63	40–79	Defecation sites	Davies and Jarvis, 1986
Bathyergus	1	71.2–165	9–15.83	45	1–5	Circular; 25	40–58	Sleeping	Herbst and Bennett, 2006
" "	" "	–	–	–	1–2	–	40–55	Food stores	Herbst and Bennett, 2007
Cryptomys	3	380; excludes side branches; greater than 0.4 km with side branches	5–7	25–30	2	Avg. Diameter: 15 Avg. length: 17	40–44	Sleeoping/eating	Davies and Jarvis, 1986
" "	" "	–	–	–	5	6.5	13–58	Food stores	Davies and Jarvis, 1986
Cryptomys (Mesic site)	2–8	50–200	3.7–8.5	13–34	–	–	–	–	Spinks et al. (2000)
Cryptomys (Arid site)	2–9	150–510	2.9–8.7	6.2–26.5	–	–	–	–	Spinks et al. (2000)

wo localities, referred to as the Museum and Tuzigoot, of burrows excavated by the pocket gopher *Thomomys bottae* were investigated by Reichman et al. (1982). The burrows are occupied by one individual, but a male and a female may share a chamber during the breeding season, some of which chambers have been found at 1.6 m deep (Fig. 51). The burrow lengths are greater in reproductive males then females. Average measurements of the Museum locality of individual burrows comprise tunnels with a length of 63.2 m with 21 branches that are 1.45 m long. The area that an individual burrow system covered was 34.6 m^2. The average measurements of the burrows in the Tuzigoot locality comprise tunnels 31.6 m long with 13.4 branches that are 1.51 m long. The area that an individual burrow system covered was 35.5 m^2.

Fossil rodents.—Burrows from the Miocene of the Pawnee Creek Formation of northeastern Colorado are assigned to the ichnotaxa *Alezichnos chelecharatos* (Gobetz, 2006) (Fig. 52). Tunnels are ovate in cross section ranging 9.4–20.2 cm in height and 11.9–22 cm wide. Tunnels are sinuous in architecture, undulate in a horizontal plan, and often branch into two or more divisions. Shorter tunnels range from 30–60° degrees from the horizontal. Scratch marks in sets of two or three are found on the end and side walls of the tunnels (Fig. 52A). Scratch marks generally curve upward from tunnel floors away from the terminus at a 25° angle. At the terminus scratch marks diverge from the midline and occur around the side walls. Knobs with scratch marks dug out by the rodent are commonly found along the tunnel walls.

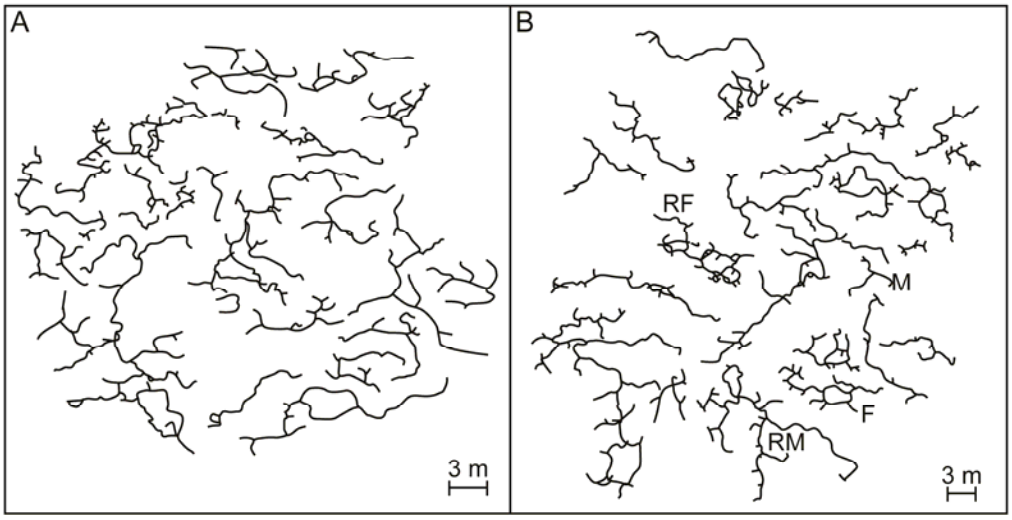

FIGURE 51—Plan view of pocket gopher burrow systems at two localities. A). Museum locality; B). Tuzigoot locality showing burrow systems of reproductive males and females compared to nonreproductive males and females. Only one burrow system of each labeled. RM = Reproductive male; RF = Reproductive female; M = Nonreproductive male; F = Nonreproductive female.

Burrows from the early Miocene Harrison Formation, Nebraska are assigned to the ichnotaxa *Alezichnos trogodont* (Gobetz and Martin, 2006). The burrows are tubular and sinuous, varying in directionality, have an irregular orientation, and are parts of a rambling labyrinthine system with complex branching tunnels. Some tunnels are weakly helical in the vertical plane. Cross sectional diameter ranges from 5.6–6.7 cm, and cross sections vary from wider dorsoventrally to wider transversely. The holotype specimen (KU 133009) has a bilobate chamber at one end. The surficial morphology of the burrows comprises incisor parks described as paired, flat edge grooves on the dorsal surface and sides of the burrows. Some paired grooves form chevrons. Scratch marks are found mainly on the bilobate terminal chamber. Scratch marks also occur on knob like projections found on the walls of the burrow.

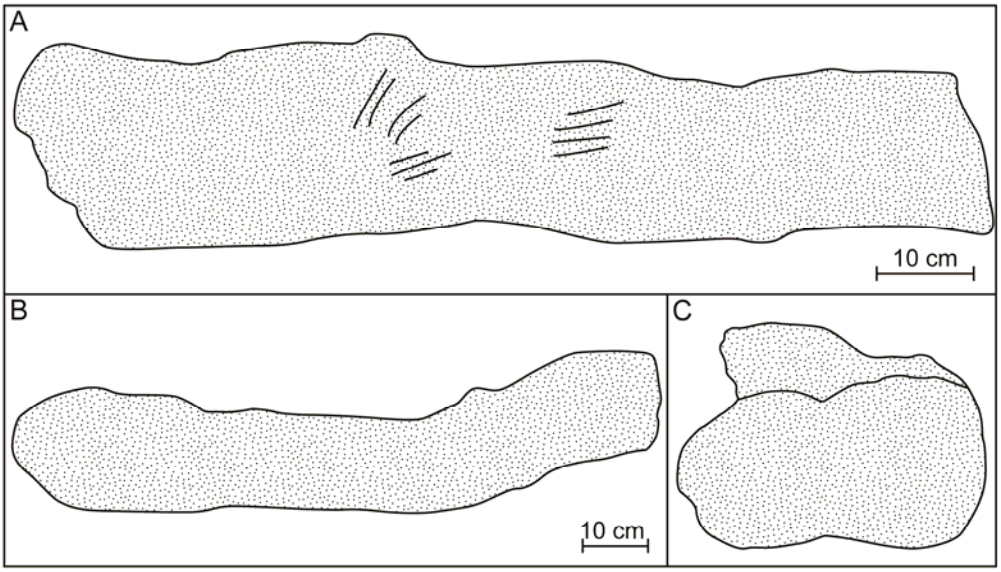

FIGURE 52—Burrow morphology of *Alezichnos chelecharatos*. Burrow was possibly excavated by a mylagaulid. A). Side view of *A. chelecharatos* tunnel with some scratch marks shown on the surface. B). Top view of same *A. chelecharatos* tunnel. C). Bilobate terminus of *A. chelecharatos* tunnel. Bilobate terminus on left hand side of tunnel in A.

Burrows from the Miocene Harrison Formation in western Nebraska and Eastern Colorado were first described by Barbour (1892) as fresh water sponges and then a new plant fossil, and assigned the trace fossil the name *Daimonelix* meaning devils corkscrew. Martin and Bennett (1977) give a detailed description of these burrows and report the presence of skeletons of the small beaver *Paleocastor* in *Daimonelix*. They attribute the excavation of *Daimonelix* to *Paleocastor* and relate the surficial structures of the burrow to the morphology and behavior of the beavers. *Daimonelix* is characterized by a single entrance with a bulbous turnaround just below, vertically oriented helical tunnels, and a lower living terminal chamber (Fig. 53). Fragmentary evidence of a funnel shaped inner wall indicates there may have been a mound associated with the entrance.

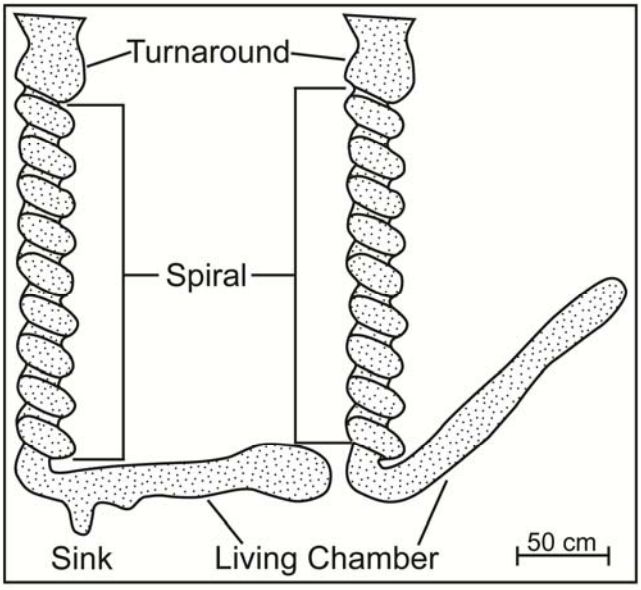

FIGURE 53—Burrow morphology of *Daimonelix*. Note the two different living chambers. Modified from Martin and Bennett (1977).

Burrows that belonged to *Paleocastor fossor* contained 6 to 12 coils with an average of about nine. Within the individual spirals the shafts are uniform in diameter with cross sections that are nearly circular with diameters ranging from 11–14 cm. The angle of inclination ranges from 25–30°. The shaft diameter widens after the lowermost coil where it enters an upwardly inclined living terminal chamber ranging from 2–37°. The living chambers with inclinations over 30° tended to be simple, however those with lower inclinations had short side chambers, or vertical sinks dug into floor, and some are greatly expanded in the horizontal plane (Fig. 53). *Daimonelix* extended ~2.1–2.75 m below the surface. The surficial morphology of the burrows comprises hundreds of claw marks commonly found on the floor and sides of the burrows. The upper surface of the burrow had the greatest proportion of incisor marks. A single larger burrow

also found in the Harrison Formation with a coil diameter of 21 cm is believed to belong to *Paleocastor magnus*.

FIGURE 54—Mammal burrows in the Lower Jurassic Navajo Sandstone assigned to the ichnotaxa *Labyrinthopolis odieri*. A). High density burrows with Y- and T-interconnected elements. B). Sinuous burrow leading to a chamber. C). Burrow tunnel that leads to a chamber. D). Various burrow elements that are curved. E). Cross section of burrow showing flat floor and curved roof. F). Burrow that shows Y-branching.

Burrows from the Miocene Pawnee Creek Formation in Colorado are assigned to the ichnotaxa *Polychoredrites tetrachelichnus* (Hembree and Hasiotis, 2008). These burrows are characterized by complex systems of interconnected subhoriztontal and subvertical tunnels. Tunnels curve downward from the surface at 10–20° to a terminal chamber. Side branches lead to smaller chambers. The tunnel systems extend laterally 1.5–1.7 m to a depth of 1.1 m. The cross sections are elliptical in shape with widths of 12–15 cm and heights of 5–8 cm. The terminal chambers are 15–20 cm in diameter. Surficial morphology of the burrow walls comprises a series of three to four long parallel scratch marks.

Burrows found below interdune deposits of the Lower Jurassic Navajo Sandstone are assigned to the ichnotaxa *Labyrinthopolis odieri* (Fig. 54). *L. odieri* occurs both as float and more commonly in place as full relief casts. *L. odieri* are infilled with fine-grained sand with no internal structure or lining. *L. odieri* exhibits complex architecture of high-density, interconnected elements with Y- and T-branching, sinuous tunnels, ramps, and chambers in mound-like areas, or in areas pervasive over the entire outcrop. At one locality mounds are clearly distinguishable and range in dimension from 40 m by 40 m to 10 m by 15 m and are ~1 m in height. Orientations of *L. odieri* are horizontal to subhorizontal with ramps measuring 6–60º (average = 24º), from horizontal. *L. odieri* have predominately flat bottoms, a rounded top, and

are flattened dorsoventrally. Dimensions of *L. odieri* ranged from 4.23 to 21 cm wide and 1.16 to 10.22 cm high (average = 9.3 cm wide and 4.2 cm high). Interconnected tunnels form Y and T branches with wider dimensions than the tunnels themselves, and comprised angles of branching from 40 to 160º (average = 97º) (Fig. 54A, F).

Surficial morphology features comprise scallop marks paired on the sides of *L. odieri* produced from the organism's claw pushing sediment out on the walls of the burrow. Widths measured from trough to trough of scallops range from 5 to 7 cm (average = 6.4 cm); the scallops protrude outward 0.5–1.5 cm (average = 1 cm) from the surface. Other biogenic structures preserved on the walls and within the burrows included rhizoliths and invertebrate burrows. Rhizoliths are often smaller in diameter, and are composed of carbonate different in color with respect to the buff colored *L. odieri*. Invertebrate burrows are preserved as negative and positive relief, randomly oriented cylinders on the burrow walls.

Summary of mammal burrows

Ancient and extant mammal burrows show the greatest difference in complexity compared to the other groups. Carnivores or other large mammals tend to construct simple burrows that comprise a single tunnel that leads to a chamber at the end. In some cases the large mammals occupy other mammals burrows and slightly modify them for what they need. The fossil burrows found in the Pawnee Creek Formation thought to be excavated by an animal in the Mustelidae family showed increased complexity owing to its helical architecture.

Members in the rodent family show the greatest amount of complexity in burrow systems. This complexity can arise from several factors such as the social structure, the proximity of food, and the proximity of potential mates. Burrows typically had one or more

entrances to the surface with surface mounds. Underground was an interconnecting network of ramps that lead to helical, sinuous, and straight tunnels and shafts, and one or more chambers. Burrow systems also may have the short blindly ending bolt holes to hide from predators. Complexity, length, and size of the burrows increased with increased social structure relating to the number of individuals that lived in the burrow systems, and also if the food was sparse such as in arid environments. *Daimonelix*, excavated by the beaver *Paleocastor*, did not branch, but was helical in architecture until the tunnels ends in a living chamber.

ENIGMATIC BURROWS

Burrows found in the eolian cross strata of the upper half of the Escalante Member of the Entrada Sandstone in southern Utah are interpreted to be excavated by large vertebrates (Loope, 2006) (Fig. 55). These burrows were likely produced by animals digging into rain-moistened, cohesive sand and may have served as temporary shelters from the extreme temperatures. Burrows occur in clusters at second- and third-order bounding surfaces that are inclined from 16–22° from surface of origin. Burrows are typically cylindrical with diameters from 28 to 63 cm wide (average = 41 cm) and maximum lengths from 51 to 305 cm (average = 141 cm). One burrow ended in an enlarged chamber ~63 cm in diameter. Three different materials infill the burrows: cross strata, breccias, and structureless sand. Cross strata was interpreted as sand drifts migrating into the abandoned burrow, whereas breccias and structureless sand were generated by roof collapse. This burrow has morphologies similar with those described of therapsids and larger reptiles such as the crocodiles.

Two types of burrows constructed by tetrapods are found in the Triassic of Antarctica (Sidor et al., 2008). The first burrow, designated tetrapod ichnogenus A, is a giant terminal

chamber from the Lower Fremouw Formation (Fig. 56A). The burrows maximum dimensions are ~15.7 cm wide, 8.5 cm tall, and 34.8 cm long and tapers distally. The dorsal part of the burrow is domed and has a smooth surface, the ventral surface has two broad, parasagitally aligned lobes separated by trough when viewed in cross section (Fig. 56A). This trough is similar to other burrows that have a raised floor creating a bilobate morphology. The surficial morphology of the burrows comprises scratch marks rising ventral to dorsally three quarters of the way up the lateral face oriented ~20° to the horizontal when viewed in lateral view.

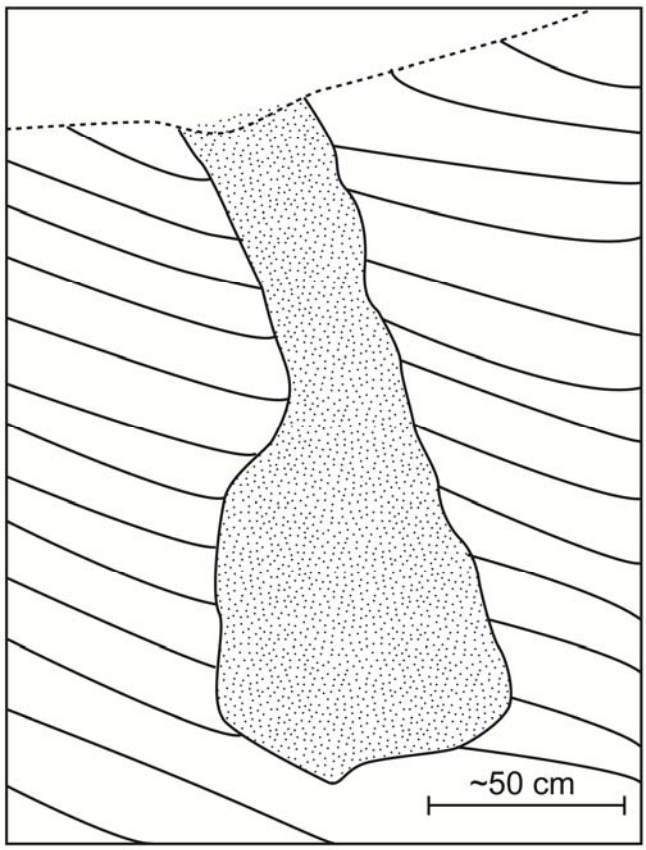

FIGURE 55—Morphology of a burrow in the Entrada Sandstone. Dotted line represents a 2nd order bounding surface and curved lines represent eolian cross stratification. Modified from Loope (2006).

The burrow designated tetrapod ichnogenus B is found in the Lashly Formation in Antarctica (Fig. 56B). A total of nine specimens were collected that have a rounded dorsal surface and a ventral surface with two lobes separated by a trough that creates a bilobate morphology (Figs. 55B–C). The cross sections of the burrows are wider then they are high with dimensions ranging from 4.32–6.01 cm wide, 2.46–3.94 cm high, averaging 5 cm wide and 3 cm high. The lengths although incomplete ranged from 7.36–43.5 cm. The surficial morphology of the burrows comprises scratch marks mostly visible on the ventral surface and oriented longitudinally, but angled ~20° to the horizontal on the lateral surface. These burrows have morphologies that are most similar to therapsid burrows that are found also in Antarctica as well as South Africa.

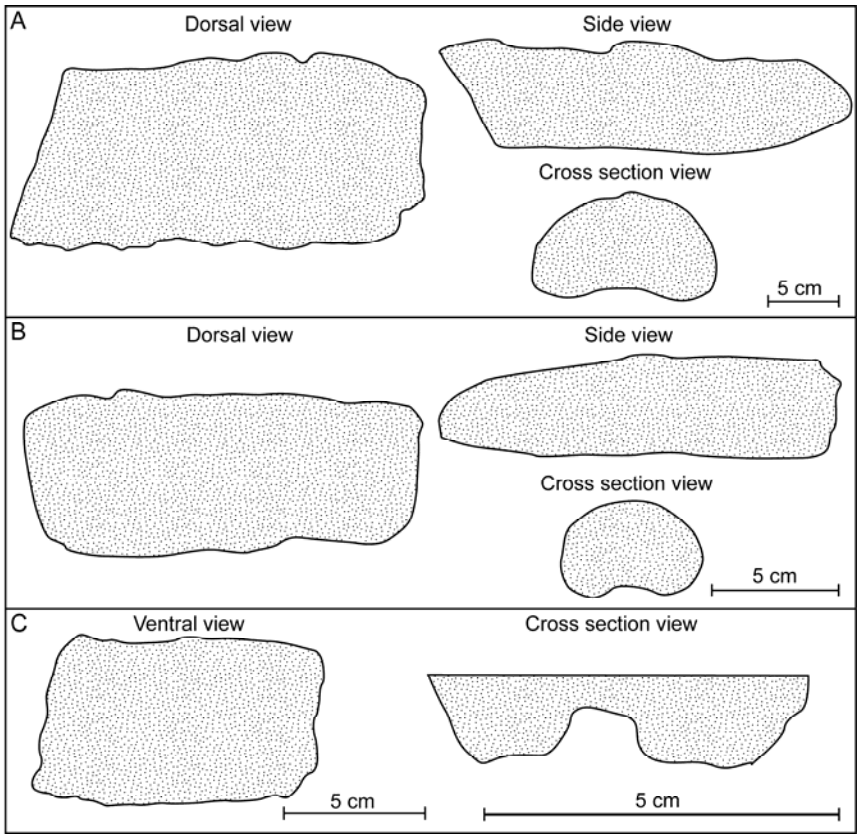

FIGURE 56—Burrow morphology of two types of burrows from Antarctica. A). Terminal chamber of tetrapod ichnogenus A. B). possible terminal chamber of tetrapod ichnogenus B. C). Ventral and cross sectional view of a tunnel from tetrapod ichnogenus B. Modified from Sidor et al. (2008).

CONCLUSIONS AND FUTURE DIRECTION

There is a wide spectrum of burrow morphologies that are seen between the groups of vertebrates. Burrow morphologies within the groups can also be different; however, some do show consistent morphologies that are seen in the fossil and extant specimens. There are three important reasons why it is important to study and document the wide array of burrow morphologies of vertebrates. First is to help correctly identify vertebrate burrows in the fossil record from other abiogenic origins. Recently the number of fossil vertebrate burrows has increased, and there are likely many out there that have been identified incorrectly or overlooked as vertebrate in origin. There may also be structures out there that were incorrectly identified as fossil vertebrate burrows. The number of fossil burrows incorrectly identified in origin may be great because of not recognizing the morphologies of a vertebrate burrow, or assuming that a vertebrate could not have excavated a burrow in an environment. Second is to correctly identify the excavator if body fossils are not found. The body fossil record of particular vertebrates is poor, and can especially poor in specific environments. A vertebrate burrow can represent a hidden biodiversity in an environment or even extend the range that a particular group has lived. Third, correct identification of a vertebrate burrow as well as the excavator can help in interpretations of the paleoenvironment. Some vertebrates will only excavate burrows in particular environments, or the burrow the vertebrate create tells something specific about the environment. An example is the lungfish that excavated aestivation burrows in muddy

environments that experience wet and dry conditions. If many lungfish burrows are found overlapping one another, this represents many generations in the wet and dry environment.

In order to meet this goal of documenting vertebrate burrow morphologies, much work still needs to be done. Neoichnological experiments and descriptions of burrows in the field of all the vertebrates need to be done because many vertebrates do not have much literature on the burrow morphologies. Additional information can also be gathered for those vertebrates that have much literature on the burrow morphologies to increase knowledge that can lead to new discoveries. Special care also needs to be done on documenting burrows in variable conditions such as media consistency, social structure, or food availability. Burrow morphologies within particular groups can change drastically based on variable conditions.

ACKNOWLEDGEMENTS

We thank L. Martin for discussions on vertebrate burrows and of knowledge of extant and fossil vertebrate fauna. We are thankful for reviews from XXX and XXX that improved this manuscript.

REFERENCES

ANDERSON, M.D., and RICHARDSON, P.R.K., 2005, The physical and thermal characteristics of aardwolf dens: South African Journal of Wildlife Research, v. 35, p. 147–153.

ATKINSON, R.J.A., and PULLIN R.S.V., 1996, Observations on the burrows and burrowing behavior of the red band-fish, *Cepola rubescens* L: Marine Ecology, v. 17, p. 23–40.

ATKINSON, R.J.A., and TAYLOR, A.C., 1991, Burrows and burrowing behavior of fish, *in* Meadows, P.S., and Meadows, A., eds., The environmental impact of burrowing animals and animal burrows, Clarendon Press, Oxford, p. 133–155.

ATKINSON, R.J.A., PULLIN, R.S.V., and DIPPER, F.A., 1977, Studies on the Red band fish, *Cepola rubescens*: Journal of Zoology (London), v. 182, p. 369–384.

ATKINSON, R.J.A., PELSTER, B., BRIDGES, C.R., TAYLOR, A.C., and MORRIS, S., 1987, Behavioral and physiological adaptations to a burrowing lifestyle in the snake blenny, *Lumpenus lampretaeformis*, and the red band-fish, *Cepola rubescens*: Journal of Fish Biology, v. 31, p. 639–659.

AUFFENBERG, W., and WEAVER, W.G., JR., 1969, *Gopherus berlandieri* in southeastern Texas: Bulletin of the Florida State Museum, Biological Science Series, v. 13, p. 141–203.

BAILEY, W.J., and ROBERTS, J.D., 1981, The bioacoustics of the burrowing frog *Heleioporus* (Leptodactylidae): Journal of Natural History, v. 15, p. 693–702.

BARBOUR, E.H., 1892, Notice of new gigantic fossils: Science, v. 19, p. 99-100.

BOUILLON, J., 1961, The lungfish of Africa: Natural History, v.70, p. 57–76.

BRAGG, A.N., 1944, The spadefoot toads in Oklahoma with a summary of our knowledge of the group: The American Naturalist, v. 78, p. 517–533.

BURGER, J., and GOCHFELD, M., 1991, Burrow site selection by black iguana (*Ctenosaura similis)* at Palo Verde, Costa Rica: Journal of Herpetology, v. 25, p. 430–435.

BURNS, J.A., FLATH, D.L., and CLARK, T.W., 1989, On the structure and function of white-tailed prairie dog burrows: Great Basin Naturalist, v. 49, p. 517–524.

CARLSON, K.J., 1968, The skull morphology and aestivation burrows of the Permian lungfish, *Gnathorhiza serrata*: Journal of Geology, v. 76, p. 62–71.

CARROLL, R.L, 1965, Lungfish burrows from the Michigan Coal Basin: Science, v. 148, p. 963–964.

CARTER, G.S., and BEADLE, L.C., 1930, Notes on the habits and development of *Lepidosiren paradoxa*: Journal of Linnean Society Zoology, v. 37. p. 197–203.

CLAYTON, D.A., and VAUGHAN, T.C., 1986, Territorial acquisition in the mudskipper *Boleophthalmus boddarti* (Teleostei, Gobiidae) on the mudflats of Kuwait: Journal of Zoology (London), v. 209, p. 501–519.

COLIN, P.L., 1973, Burrowing behavior of the yellowhead jawfish, *Opistognathus aurifrons*: Copeia, v. 1973, p. 84–90.

COLIN, P.L., and ARNESON, D.W., 1978, Aspects of the natural history of the swordtail jawfish, *Lonchopisthus micrognathus* (Poey) (Pisces: Opistognathidae), in south-western Puerto Rico: Journal of Natural History, v. 12, p. 689–697.

DAMIANI, R., MODESTO, S., YATES, A., and NEVELING, J., 2003, Earliest evidence of cynodont burrowing: Proceedings of the Royal Society of London, v. 270, p. 1747–1751.

DAVIES, K.C., and JARVIS, J.U.M., 1986, The burrow systems and burrowing dynamics of the mole–rats *Bathygergus hottentotus* in the fynbos of the south–western Cape, South Africa: The Zoological Society of London, v. 209, p. 125–147.

DUCEY, P.K., FORMANOWICZ, D.R., JR., BOYET, L., MAILLOUX, J., and NUSSBAUM, R.A., 1993, Experimental examination of burrowing behavior in caecilians (Amphibia:Gymnophiona): effects of soil compaction on burrowing ability of four species: Herpetologica, v. 49, p. 450–457.

ETHERIDGE, K., 1990, Water balance in estivating sirenid salamanders (*Siren lacertian*): Herpetologica, v. 46, p. 400–406.

EMERSON, S.B., 1976, Burrowing in frogs: Journal of Morphology, v. 149, p. 437–458.

FALCON-LANG, H.J., BENTON, M.J., and STIMSON, M., 2007, Ecology of earliest reptiles inferred from basal Pennsylvanian trackways: Journal of the Geological Society, London, v. 164, p. 1113–1118.

FRASER, N.C., 1988, The osteology and relationships of *Clevosaurus* (Reptilia: Sphenodontida): Philosophical Transactions of the Royal Society of London. Series B. Biological Sciences, v. 321, p. 125–178.

FREEMAN, J.R., 1958, Burrowing in the salamanders *Pseudobranchus striatus* and *Siren lacertiana*: Herpetologica, v. 14, p. 130.

GANS, C., 1969, Amphisbaenians: reptiles specialized for a burrowing existence: Endeavour, v. 28, p. 146–151.

GANS, C., 1973, Locomotion and burrowing in limbless vertebrates: Nature (London), v. 242, p. 414–415.

GANS, C., 1974, Biomechanics: an approach to vertebrate biology: Philadelphia, J.B. Lippincott Company, 261 p.

GANS, C., 1978, The characteristics and affinities of the Amphisbaeni: Zoological Society of London, Transactions, v. 34, p. 347–416.

GILLINGHAM, J.C., CARMICHAEL, C., and MILLER, T., 1995, Social behavior of the tuatara, *Sphenodon punctatus*: Herpetological Monographs, v. 9, p. 5–16.

GOBETZ, K.E., 2006, Possible burrows of mylagaulids (Rodentia: Aplodontoidea: Mylagaulidae) from the late Miocene (Barstovian) Pawnee Creek Formation, northeastern Colorado: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 237, p. 119–136.

GOBETZ, K.E., and MARTIN, L.D., 2006, Burrows of a gopher-like rodent, possibly Gregorymys (Geomyoidea: Geomyidae: Entoptychtinae), from the early Miocene Harrison Formation, Nebraska: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 237, p. 305–314.

GREENWOOD, P.H., 1986, The natural history of lungfishes, *in* Bemis, W.E., Burggren, W.W., and Kemp, N.E., eds., The Biology and Evolution of Lungfishes: Journal of Morphology Supplement, v. 1, p. 163–179.

GROENEWALD, G.H., WELMAN, J., and MACEACHERN, J.A., 2001, Vertebrate burrow complexes from the early Triassic Cynognathus Zone (Driekoppen Formation, Beaufort Group) of the Karoo Basin, South Africa: Palaios, v. 16 p. 148–160.

HALLINAN, T., 1923, Observations made in Duval County, northern Florida, on the gopher tortoise (*Gopherus polyphemus*): Copeia, p. 11–20.

HANSEN, K.L., 1963, The burrow of the gopher tortoise: Quarterly Journal of the Florida Academy of Sciences, v. 26, p. 353–360.

HASIOTIS, S.T., 2002, Continental trace fossils: SEPM Short Course Notes, v. 51 p. 1–132.

HASIOTIS, S.T., and BOURKE, M.C., 2006, Continental trace fossils and museum exhibits: displaying burrows as organism behavior frozen in time: The Geological Curator, v. 8, p. 211–226.

HASIOTIS, S.T., MITCHELL, C.E., and DUBIEL, R.F., 1993, Application of morphologic burrow interpretations to discern continental burrow architects: lungfish or crayfish: Ichnos, v. 2, p. 315–333.

HASIOTIS, S.T., WELLNER, R.W., MARTIN, A., DEMKO, T.M., 2004, Vertebrate burrows from Triassic and Jurassic continental deposits of North America and Antarctica: their paleoenvironmental and paleoecological significance: Ichnos, v. 11, p. 103–124.

HASIOTIS, S.T., PLATT, B.F., HEMBREE, D.I., and EVERHEART, M.J., 2007, The trace-fossil record of vertebrates, *in* Miller, W. III., ed., Trace Fossils—Concepts, Problems, Prospects: Elsevier Press, Amsterdam, p. 196–218.

HEMBREE, D.I., and HASIOTIS, S.T., 2006, The identification and interpretation of reptile ichnofossils in paleosols through modern studies: Journal of Sedimentary Research, v. 76, p. 575–588.

HEMBREE, D.I., and HASIOTIS, S.T., 2008, Miocene vertebrate and invertebrate burrows defining compound paleosols in the Pawnee Creek Formation, Colorado, U.S.A: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 270, p. 349–365.

HEMBREE, D.I., HASIOTIS, S.T., and MARTIN, L.D., 2004, Amphibian burrows and ephemeral ponds of the Lower Permian Speiser Shale, Kansas: evidence for seasonality in the midcontinent: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 203, p. 127–152.

HEMBREE, D.I., HASIOTIS, S.T., and MARTIN, L.D., 2005, *Torridorefugiumeskridgensis* (new ichnogenus and ichnospecies): Amphibian aestivation burrows from the Lower Permian Speiser Shale of Kansas: Journal of Paleontology, v. 79, p. 583–593.

HICKMAN, C.G., 1990, Adaptiveness of tunnel system features in subterranean mammal burrows, *in* Nevo, E., Reig, O.A., eds., Evolution of Subterranean Mammals at the Organismal and Molecular Levels: Wiley-Liss, New York, p. 185–210.

HILDEBRAND, M., 1974, Analysis of Vertebrate Structure: John Wiley and Sons, New York, 710 p.

HUNT, R.M., XIANG-XU, X., and KAUFMAN, J., 1983, Miocene burrows of extinct bear dogs: indications of early denning behavior of large mammalian carnivores: Science, v. 221, p. 364–366.

JARVIS, J.U.M., and SALE, J.B., 1971, Burrowing and burrow patterns of east African mole–rats *Tachyoryctes, Heliophobius, Heterocephalus*: Journal of Zoology London, v. 163, p. 451–479.

JOHNELS, A.G., and SVENSSON, G.S.O., 1954, On the biology of *Protopterus annectens* (Owens): Arkiv for Zoologi, vol. 7, p. 131–164.

KERR, J.G., 1988, On the dry-season habitats of *Lepidosiren*: Proclamation of Zoological Society of London, p. 41–44.

KIELAN-JAWOROWSKA, Z., CIFELLI, R.L., and LUO, Z., 2004, Mammals from the Age of Dinosaurs: Origins, Evolution, and Structure: Columbia University Press, New York, 630 p.

KINLAW, A., 1999, A review of burrowing by semi-fossorial vertebrates in arid environments: Journal of Arid Environments v. 41, p. 127–145.

KINLAW, A.E., CONYERS, L.B., and ZAJAC, W., 2007, Use of ground penetrating radar to image burrows of the gopher tortoise (*Gopherus polyphemus*): Herpetological Review, v. 38, p. 50–56.

LEE, A.K., and MERCER, E.H., 1967, Cocoon surrounding desert-dwelling frogs: Science, v. 157, p. 87–88.

LOOPE, D.B., 2006, Burrows dug by large vertebrates into rain-moistened Middle Jurassic dunes: The Journal of Geology, v. 114, p. 753–762.

LOOPE, D.B., 2008, Life beneath the surface of active Jurassic dunes: burrows from the Entrada Sandstone of south-central Utah: Palaios, v. 23, p. 411–419.

LUCAS, S.G., GOBETZ, K.E., ODIER, G.P., MCCORMICK, T., and EGAN, C., 2006, Tetrapod burrows from the Lower Jurassic Navajo Sandstone, Southeastern Utah: New Mexico Museum of Natural History and Science, Bulletin 37, p. 147–154.

MACAVOY, E.S., MCGIBBON, L.M., SAINSBURY, J.P., LAWRENCE, H., WILSON, C.A., DAUGHERTY, C.H., and CHAMBERS, G.K., 2007, Genetic variation in island populations of tuatara (*Sphenodon* spp) inferred from microsatellite markers: Conservation Genetics, v. 8, p. 305–318.

MANKIN, P.C., and GETZ, L.L., 1994, Burrow morphology as related to social organization of *Microtus ochrogaster*: Journal of Mammalogy, v. 75, p. 492–499.

MARKWELL, T.J., 1997, Video camera count of burrow-dwelling fairy prions, sooty shearwaters, and tuatara on Takapourewa (Stephens Island), New Zealand: New Zealand Journal of Zoology, v. 24, p. 231–237.

MARTIN, L.D., and BENNETT, D.K., 1977, The burrows of the Miocene beaver *Palaeocastor*, western Nebraska, U.S.A: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 22, p. 173–193.

MAYES, P.J., 2007, The use of burrows and burrow characteristics of the semi-aquatic *Varanus mertensi* (Reptilia: Varanidae): Mertensiella, v. 16, p. 312–321.

MCALLISTER, J., 1988, Lungfish burrows in the Upper Triassic Chinle and Dolores Formations, Colorado Plateau-Comments on the recognition criteria of fossil lungfish burrows: Journal of Sedimentary Petrology, v. 58, p. 365–367.

MCCLANAHAN, L.L. JR., SHOEMAKER, V.H., AND RUIBAL, R., 1976, Structure and function of the cocoon of a Ceratophryd frog: Copeia, v. 1976, p. 179–185.

MILLER, M.F., HASIOTIS, S.T., BABOCK, L.E., ISBELL, J.L., and COLLINSON, J.W., 2001, Tetrapod and large burrows of uncertain origin in Triassic high paleolatitude floodplain deposits, Antarctica: Palaios, v. 16, p. 218–232.

MULDER, C.P.H., and KEALL, S.N., 2001, Burrowing seabirds and reptiles: impacts on seeds, seedlings, and soils in an island forest in New Zealand: Oecologia, v. 127, p. 350–360.

NEVO, E., 1999, Mosaic Evolution of Subterranean Mammals: Regression, Progression, and Convergence: Oxford University Press, New York, 413 p.

NEWMAN, D.G., 1987, Burrow use and population densities of tuatara (*Sphenedon punctatus*) and how they are influenced by fairy prions (*Pachyptila turtur*) on Stephens Island, New Zealand: Herpetologica, v. 43, p. 336–344.

NORRIS, K.S., 1953, The ecology of the desert iguana *Dipsosaurus dorsalis*: Ecology, v. 34, p. 265–287.

OLSON, E.C., and BOLLES, K., 1975, Permo-Carboniferous fresh water burrows: Fieldiana Geology, v. 33, p. 271–290.

PENNA, M., and SOL′IS, R., 1996, Influence of burrow acoustics on sound reception by frogs *Eupsophus* (Leptodactylidae): Animal Behaviour, v. 51, p. 255–263.

PENNA, M., and SOL′IS, R., 1999, Extent and variation of sound enhancement inside burrows of the frog *Eusophus emiliopugini* (Leptodactylidae): Behavioral Ecology and Sociobiology, v. 47, p. 94–103.

PINDER, A.W., STOREY, K.B., and ULTSCH, G.R., 1992, Estivation and hibernation. *in* Feder, M.E., and Burggren, W.W., eds., Environmental physiology of amphibians: University of Chicago Press, Chicago, p. 250–274.

POOLEY, A.C., 1969. The burrowing behavior of crocodiles: Lammergeyer, v. 10, p. 60–63.

RAND, A.S., and DUGAN, B., 1983, Structure of complex iguana nests: Copeia, v. 1983, p. 705–711.

REICHMAN, O.J., and SMITH, S.C., 1990, Burrows and burrowing behavior by mammals, *in* Genoways, H.H., ed., Current Mammalogy: Plenum Press, New York, p. 197–244.

REICHMAN, O.J., WHITHAM, T.G., and RUFFNER, G.A., 1982, Adaptive geometry of burrow spacing in two pocket gopher populations: Ecology, v. 63, p. 687–695.

RENO, H.W., GEHLBACH, F.R., and TURNER, R.A., 1972, Skin and aestivational cocoon of the aquatic amphibian, *Siren* intermedia le conte: Copeia, v. 1972, p. 625–631.

RICE, A.L., and JOHNSTONE, A.D.F., 1972, The burrowing behavior of the Gobiid fish *Lesueurigobius friesii* (Collett): Zeitschrift für Tierpsychologie, v. 30, p. 431–438.

RIESE, D.J., HASIOTIS, S.H., and ODIER, G., 2011, Synapsid burrows and associated trace fossils in the lower Jurassic Navajo Sandstone, southeastern, Utah, U.S.A., indicates a diverse community living in a wet desert ecosystem: *in press.*

ROMER, A.S., and OLSON, E.C., 1954, Aestivation in a Permian lungfish: Breviora, v. 30, p. 1–8.

RUIBAL, R., and HILLMAN, S., 1981, Cocoon structure and function in the burrowing Hylid frog, *Pternohyla fodiens*: Journal of Herpetology, v. 15, p. 403–408.

SIDOR, C.A., MILLER, M.F., and ISBELL, J.L., 2008, Tetrapod burrows from the Triassic of Antarctica: Journal of Vertebrate Paleontology, v. 28, p. 277–284.

SMITH, H.M., 1956, Handbook of amphibians and reptiles of Kansas: University of Kansas, Lawrence, 356 p.

SMITH, R.M.H., 1987, Helical burrow casts of therapsid origin from the Beaufort Group (Permian) of South Africa: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 60, p. 155–170.

SPINKS, A.C., and BENNETT, N.C., JARVIS, J.U.M., 2000, A comparison of the ecology of two populations of the common mole-rat, *Cryptomys hottentotus hottentotus*: the effect of aridity on food, foraging and body mass: Oecologia, v. 125, p. 341–349.

STEBBINS, R.C., and COHEN, N.W., 1995, A Natural History of Amphibians: Princeton University Press, Princeton, 316 p.

TALANDA, M., DZIĘCIOL, S., SULEJ, T., and NIEDŹWIEDZKI, G., 2011, Vertebrate burrow system from the Upper Triassic of Poland: Palaios, v. 26, p. 99–105.

TRAEHOLT, C., 1995, Notes on the burrows of the water monitor lizard, *Varanus salvator*: Malayan Nature Journal, v. 49, p. 103–112.

VOORHIES, M.R., 1975, Vertebrate burrows, *in* Frey, R.W., eds., The Study of Trace Fossils: Spring-Verlag, New York, p. 325–350.

WAKE, M.H., 1993, The skull as a locomotor organ, *in* Hanken, J., and Hall, B.K., eds., The Skull. Volume 3: Functional and Evolutionary Mechanisms: The University of Chicago Press, Chicago, p. 197–240.

CHAPTER 5. CONCLUSIONS

A wide spectrum of burrow morphologies exists between and within groups of vertebrates. The reason for the variety in morphology is the type of organism and its excavation method(s), number of individuals living the in the structure, media consistency, food availability, and reason for burrowing. Although there can be many differences in burrow morphologies, similarities can also be seen between and within fossil and extant groups. Three important reasons justify the importance for studying and documenting burrow morphologies of fossil and extant vertebrates: (1) identify fossil vertebrate burrows from other abiogenic origins; (2) identify the excavator if body fossils are not found; and (3) interpret the paleoenvironmental and paleoecological significance of the burrow. The number of fossil vertebrate burrows recently identified in the rock record has increased, and there are likely many more that have been identified incorrectly or overlooked as vertebrate in origin. There may also be structures that have been identified incorrectly as vertebrate burrows. The body fossil record of vertebrates is poor, and can be especially poor in specific environments such as in eolian environments. Owing to the greater preservation potential of trace fossils, a trace fossil can represent hidden biodiversity when body fossils of the excavator are not present in that deposit, or even extend the temporal range that a particular group has lived. Trace fossils can also provide information on the paleoenvironment and paleoecology. Some vertebrates, for example, will only excavate burrows in specific environments, and the burrow morphology reflects specific physicochemical conditions of the environment.

In this thesis, the origin of enigmatic structures in the Lower Jurassic Navajo Sandstone as synapsid burrows was determined by studying the architectural and surficial morphologies, as well as the texture and pattern of sedimentary fill. Identification of associated structures as well

as the behaviors represented by the burrows was also used to delineate the paleoecological and paleoenvironmental environments. The burrows either underlie or are within carbonate or mudstone beds that represent deposits of lakes or springs produced from monsoonal rains. Two major types of burrows were identified based on their architectural and surficial morphologies. The most abundant are Type I burrow casts, which are composed of a complex network of horizontal to subhorizontal, interconnected sinuous tunnels, with Y- and T-branching, helical ramps, and terminal chambers. Burrow walls are predominantly smooth; however, a few exhibit scalloped features. The Type I burrows represent a new ichnogenera and ichnospecies *Labyrinthopolis odieri*, which compares well with extant eusocial and social mole-rat and vole burrows. *Labyrinthopolis odieri* are most similar to permanent burrow systems used for foraging, nesting, raising young, and escaping predators; this ichnotaxon is assigned to polychresichnia, because the architecture represents simultaneous, multiple behaviors and uses. These burrows likely created a microclimate that modulated fluctuations of humidity and temperature compared to the surface, allowing the organism to inhabit the Navajo desert. Although no body fossils of mammals are present, the known occurrence of mammals in the Jurassic Period indicates that these burrows may represent hidden biodiversity in the Navajo Sandstone.

Type II burrow casts are rare and composed of large diameters. One of these burrows has a simple inclined tunnel with a raised floor with a bilobate morphology similar to that found in Permian and Early Triassic therapsid burrows of South Africa. Type II burrows exhibit well-preserved scratch marks on the lower and upper margin of the burrow, indicating that one large individual, most likely a therapsid, excavated them. Type II burrows represent a new ichnogenera and ichnospecies *Schemalitus psalihyponomes.* The behaviors represented by the *S. psalihyponomes* burrows are difficult to discern because only two specimens are partially

exposed. *S. psalihyponomes* are most similar to burrows constructed by alligators and monitor lizards rather than burrows constructed by mammals.

The association of *L. odieri* and *S. psalihyponomes*, along with rhizoliths, body fossils, and other invertebrate burrows demonstrates that wet interdune environments sustained life in this desert ecosystem. *L. odieri* and *S. psalihyponomes* also show evidence of organisms developing behavioral adaptations to survive in harsh environments of the Navajo desert for shelter, and *L. odieri* may also be used for food foraging. Other organisms in the Navajo desert ecosystem likely made use of the burrows excavated for either their own protection in abandoned burrows, or for nutrients buried in infilled burrows.

Opportunity for future research in the Navajo Sandstone abounds, in that much work still needs to be done at many unstudied localities in and around the Moab area. *L. odieri* and *S. psalihyponomes* burrows have recently been found but not studied in detail in the Navajo Sandstone south of Moab. Prospecting in interdune deposits preserved as siltstones and mudstones is important because of the likelihood of finding such burrows with well-preserved architectural and surficial morphologies as those of the *S. psalihyponomes*. Skeletal elements associated in deposits around the burrows may eventually be discovered with these and other large-diameter burrows in the Navajo Sandstone, and can be used as strong evidence for the excavator of the burrows. The strongest evidence for the excavator would be finding a skeleton of appropriate size and shape in the shaft, tunnels, or terminal chambers.

REFERENCES

AHLBRANDT, T.S., ANDREWS, S., and GWYNNE, D.T., 1978, Bioturbation of eolian deposits: Journal of Sedimentary Petrology, v. 48, p. 839–848.

ALONSO-ZARZA, A.M., GENISE, J.F., CABRERA, M.C., MANGAS, J., MARTIN-PÉREZ, A., VALDEOLMILLOS, A., and DORADO-VALIÑO, M., 2008, Megarhizoliths in Pleistocene aeolian deposits from Gran Canaria (Spain): Ichnological and palaeoenvironmental significance: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 265, p. 39–51.

ANDERSON, M.D., and RICHARDSON, P.R.K., 2005, The physical and thermal characteristics of aardwolf dens: South African Journal of Wildlife Research, v. 35, p. 147–153.

ATKINSON, R.J.A., and PULLIN R.S.V., 1996, Observations on the burrows and burrowing behavior of the red band-fish, *Cepola rubescens* L: Marine Ecology, v. 17, p. 23–40.

ATKINSON, R.J.A., and TAYLOR, A.C., 1991, Burrows and burrowing behavior of fish, *in* Meadows, P.S., and Meadows, A., eds., The environmental impact of burrowing animals and animal burrows, Clarendon Press, Oxford, p. 133–155.

ATKINSON, R.J.A., PULLIN, R.S.V., and DIPPER, F.A., 1977, Studies on the Red band fish, *Cepola rubescens*: Journal of Zoology (London), v. 182, p. 369–384.

ATKINSON, R.J.A., PELSTER, B., BRIDGES, C.R., TAYLOR, A.C., and MORRIS, S., 1987, Behavioral and physiological adaptations to a burrowing lifestyle in the snake blenny, *Lumpenus lampretaeformis*, and the red band-fish, *Cepola rubescens*: Journal of Fish Biology, v. 31, p. 639–659.

AUFFENBERG, W., and WEAVER, W.G., JR., 1969, *Gopherus berlanceri* in southeastern Texas: Florida State Museum Bulletin, v. 13, p. 141–203.

BAILEY, W.J., and ROBERTS, J.D., 1981, The bioacoustics of the burrowing frog *Heleioporus* (Leptodactylidae): Journal of Natural History, v. 15, p. 693–702.

BAIRD, D., 1980, A prosauropod dinosaur trackway from the Navajo Sandstone (Lower Jurassic), *in* Jacobs, L.L., ed., Aspects of Vertebrate History: Essays in Honor of Edwin Harris Colbert: Museum of Northern Arizona Press, Flagstaff, p. 219–230.

BARBOUR, E.H., 1892, Notice of new gigantic fossils: Science, v. 19, p. 99-100.

BEGALL, S., and GALLARDO, M.H., 2000, *Spalacopus cyanus* (Rodentia: Octodontidae): an extremist in tunnel constructing and food storing among subterranean mammals: Journal of Zoology (London), v. 251, p. 53–60.

BENTON, M.J., 1988, Burrowing by vertebrates: Nature, v. 331, p. 17–18.

BERTLING, M.S., BRADDY, S.J., BROMLEY, R.G., DEMATHIEU, G.R., GENISE, J., MIKULÁŠ, J.K., NIELSEN, K.S.S., RINDSBERG, A.K., SCHLIRF, M., AND UCHMAN, A., 2006, Names for trace fossils: a uniform approach: Lethaia, v. 39, p. 265–286.

BOUILLON, J., 1961, The lungfish of Africa: Natural History, v.70, p. 57–76.

BRAGG, A.N., 1944, The spadefoot toads in Oklahoma with a summary of our knowledge of the group: The American Naturalist, v. 78, p. 517–533.

BROMLEY, R.G., 1996, Trace Fossils: Biology and Taphonomy: Chapman and Hall, London, 361 p.

BOUILLON, J., 1961, The lungfish of Africa: Natural History, v.70, p. 57–76.

BOWN, T.M., and KRAUS, M.J., 1983, Ichnofossils of the alluvial Willwood Formation (Lower Eocene), Big Horn Basin, northwest Wyoming, U.S.A: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 43, p. 95–128.

BURGER, J., and GOCHFELD, M., 1991, Burrow site selection by black iguana (*Ctenosaura similis)* at Palo Verde, Costa Rica: Journal of Herpetology, v. 25, p. 430–435.

BURNS, J.A., FLATH, D.L., and CLARK, T.W., 1989, On the structure and function of white-tailed prairie dog burrows: Great Basin Naturalist, v. 49, p. 517–524.

CARLSON, K.J., 1968, The skull morphology and aestivation burrows of the Permian lungfish, *Gnathorhiza serrata*: Journal of Geology, v. 76, p. 62–71.

CARROLL, R.L., 1965, Lungfish burrows from the Michigan Coal Basin: Science, v. 148, p. 963–964.

CARTER, G.S., and BEADLE, L.C., 1930, Notes on the habits and development of *Lepidosiren paradoxa*: Journal of Linnean Society Zoology, v. 37. p. 197–203.

CLARK, J.M., MONTELLANO, M. HOPSON, J.A., HERNANDEZ, R., and FASTOVSKY, D.E., 1994, An Early or Middle Jurassic tetrapod assemblage from the La Boca Formation, northeastern Mexico, *in* Fraser, N.C., and Sues, H.-D., eds., In the Shadow of the Dinosaurs: Early Mesozoic Tetrapods: New York, Cambridge University Press, 435 p.

CLAYTON, D.A., and VAUGHAN, T.C., 1986, Territorial acquisition in the mudskipper *Boleophthalmus boddarti* (Teleostei, Gobiidae) on the mudflats of Kuwait: Journal of Zoology (London), v. 209, p. 501–519.

COLIN, P.L., 1973, Burrowing behavior of the yellowhead jawfish, *Opistognathus aurifrons*: Copeia, v. 1973, p. 84–90.

COLIN, P.L., and ARNESON, D.W., 1978, Aspects of the natural history of the swordtail jawfish, *Lonchopisthus micrognathus* (Poey) (Pisces: Opistognathidae), in south-western Puerto Rico: Journal of Natural History, v. 12, p. 689–697.

COX, G.W., 1984, The distribution and origin of Mima mound grasslands in San Diego County, California: Ecology, v. 65 p. 1397–1405.

DALQUEST, W.W., and SCHEFFER, V.B., 1942, The origin of the Mima mounds of western Washington: Journal of Geology, v. 50, p. 68–84.

DALQUEST, W.W., and CARPENTER, R.M., 1977, A new discovery of fossil lungfish burrows: Texas Journal of Science, v. 26, p. 611.

DAMIANI, R., MODESTO, S., YATES, A., and NEVELING, A., 2003, Earliest evidence of cynodont burrowing: Royal Society of London, Proceedings, v. 270, p. 1747–1751.

DAVIES, K.C., and JARVIS, J.U.M., 1986, The burrow systems and burrowing dynamics of the mole-rats *Bathygergus hottentotus* in the fynbos of the south-western Cape, South Africa: Journal of Zoology (London), v. 209, p. 125–147.

DUCEY, P.K., FORMANOWICZ, D.R., JR., BOYET, L., MAILLOUX, J., and NUSSBAUM, R.A., 1993, Experimental examination of burrowing behavior in caecilians (Amphibia:Gymnophiona): effects of soil compaction on burrowing ability of four species: Herpetologica, v. 49, p. 450–457.

EISENBERG, L., 2003, Giant stromatolites and a supersurface in the Navajo Sandstone, Capital Reef National Park, Utah: Geology, v. 31, p. 111–114.

EKDALE, A.A., and PICARD, M.D., 1985, Trace fossils in a Jurassic eolianite, Entrada Sandstone, Utah, U.S.A., *in* Curran, H.A., ed., Biogenic Structures: Their Use in Interpreting Depositional Environments: SEPM, Special Publication, v. 35, p. 3–12.

EKDALE, A.A., BROMLEY, R.G., and LOOPE, D.B., 2007, Ichnofacies of an ancient erg: A climatically influenced trace fossil association in the Jurassic Navajo Sandstone, southern Utah, USA: *in* Miller, W., III., ed., Trace Fossils—Concepts, Problems, Prospects: Amsterdam, Elsevier, p. 196–218.

EMERSON, S.B., 1976, Burrowing in frogs: Journal of Morphology, v. 149, p. 437–458.

ETHERIDGE, K., 1990, Water balance in estivating sirenid salamanders (*Siren lacertian*): Herpetologica, v. 46, p. 400–406.

FALCON-LANG, H.J., BENTON, M.J., and STIMSON, M., 2007, Ecology of earliest reptiles inferred from basal Pennsylvanian trackways: Journal of the Geological Society, London, v. 164, p. 1113–1118.

FRASER, N.C., 1988, The osteology and relationships of *Clevosaurus* (Reptilia: Sphenodontida): Philosophical Transactions of the Royal Society of London. Series B. Biological Sciences, v. 321, p. 125–178.

FREEMAN, J.R., 1958, Burrowing in the salamanders *Pseudobranchus striatus* and *Siren lacertiana*: Herpetologica, v. 14, p. 130.

GANS, C., 1969, Amphisbaenians: reptiles specialized for a burrowing existence: Endeavour, v. 28, p. 146–151.

GANS, C., 1973, Locomotion and burrowing in limbless vertebrates: Nature (London), v. 242, p. 414–415.

GANS, C., 1974, Biomechanics: an approach to vertebrate biology: Philadelphia, J.B. Lippincott Company, 261 p.

GANS, C., 1978, The characteristics and affinities of the Amphisbaeni: Zoological Society of London, Transactions, v. 34, p. 347–416.

GILLAND, J.K., 1979, Paleoenvironment of a carbonate lens in the Lower Navajo Sandstone near Moab, Utah: Utah Geology, v. 6, p. 29–37.

GILLINGHAM, J.C., CARMICHAEL, C., and MILLER, T., 1995, Social behavior of the tuatara, *Sphenodon punctatus*: Herpetological Monographs, v. 9, p. 5–16.

GOBETZ, K.E., 2005, Claw impressions in the walls of modern mole (*Scalopus aquaticus*) tunnels as a means to identify fossil burrows and interpret digging movements: Ichnos, v. 12, p. 227–231.

GOBETZ, K.E., 2006, Possible burrows of mylagaulids (Rodentia: Aplodontoidea: Mylagaulidae) from the late Miocene (Barstovian) Pawnee Creek Formation, northeastern Colorado: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 237, p. 119–136.

GOBETZ, K.E., and MARTIN, L.D., 2006, Burrows of a gopher-like rodent, possibly *Gregorymys* (Geomyoidea: Geomyidae: Entoptychtinae), from the early Miocene Harrison Formation, Nebraska: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 237, p. 305–314.

GREENWOOD, P.H., 1986, The natural history of lungfishes, *in* Bemis, W.E., Burggren, W.W., and Kemp, N.E., eds., The Biology and Evolution of Lungfishes: Journal of Morphology Supplement, v. 1, p. 163–179.

GROENEWALD, G.H., WELMAN, J., and MACEACHERN, J.A., 2001, Vertebrate burrow complexes from the early Triassic Cynognathus Zone (Driekoppen Formation, Beaufort Group) of the Karoo Basin, South Africa: Palaios, v. 16 p. 148–160.

HALLINAN, T., 1923, Observations made in Duval County, northern Florida, on the gopher tortoise (*Gopherus polyphemus*): Copeia, p. 11–20.

HANSEN, K.L., 1963, The burrow of the gopher tortoise: Quarterly Journal of the Florida Academy of Sciences, v. 26, p. 353–360.

HARSHBARGER, J.W., REPENNING, C.A., and IRWIN, J.H., 1957, Stratigraphy of the Uppermost Triassic and the Jurassic Rocks of the Navajo Country: U.S. Geological Survey, Professional Paper 291, 74 p.

HASIOTIS, S.T., 2002, Continental Trace Fossils: SEPM, Short Course Notes, 51, 132 p.

HASIOTIS, S.T., 2003, Complex ichnofossils of solitary to social soil organisms: understanding their evolution and roles in terrestrial paleoecosystems: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 192, p. 259–320.

HASIOTIS, S.T., 2004, Reconnaissance of Upper Jurassic Morrison Formation ichnofossils, Rocky Mountain Region, USA: paleoenvironmental, stratigraphic, and paleoclimatic significance of terrestrial and freshwater ichnocoenoses: Sedimentary Geology, v. 167, p. 177–268.

HASIOTIS, S.T., and BOURKE, M.C., 2006, Continental trace fossils and museum exhibits: displaying burrows as organism behavior frozen in time: The Geological Curator, v. 8, p. 211–226.

HASIOTIS, S.T., MITCHELL, C.E., and DUBIEL, R.F., 1993, Application of morphologic burrow interpretations to discern continental burrow architects: lungfish or crayfish?: Ichnos, v. 2, p. 315–333.

HASIOTIS, S.T., PLATT, B.F., HEMBREE, D.I., and EVERHEART, M.J., 2007a, The trace-fossil record of vertebrates, *in* Miller, W. III., ed., Trace Fossils—Concepts, Problems, Prospects: Amsterdam, Elsevier, p. 196–218.

HASIOTIS, S.T., ODIER, G., RASMUSSEN, D., and MCCORMICK, T., 2007b, Preliminary report on new vertebrate burrow localities in the Lower Jurassic Navajo Sandstone, Moab area, southeastern Utah: architectural and surficial burrow morphologies indicative of mammals or therapsids, and social behavior: (abstract), Geological Society of America, North-Central–South-Central Section Meeting, Lawrence, Kansas, 13 April, v. 39, p. 74.

HASIOTIS, S.T., WELLNER, R.W., MARTIN, A., and DEMKO, T.M., 2004, Vertebrate burrows from Triassic and Jurassic continental deposits of North America and Antarctica: their paleoenvironmental and paleoecological significance: Ichnos, v. 11, p. 103–124.

HEMBREE, D.I., and HASIOTIS, S.T., 2006, The identification and interpretation of reptile ichnofossils in paleosols through modern studies: Journal of Sedimentary Research, v. 76, p. 575–588.

HEMBREE, D.I., and HASIOTIS, S.T., 2008, Miocene vertebrate and invertebrate burrows defining compound paleosols in the Pawnee Creek Formation, Colorado, U.S.A: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 270, p. 349–365.

HEMBREE, D.I., HASIOTIS, S.T., and MARTIN, L.D., 2004, Amphibian burrows and ephemeral ponds of the Lower Permian Speiser Shale, Kansas: evidence for seasonality in the midcontinent: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 203, p. 127–152.

HEMBREE, D.I., MARTIN, L.D., and HASIOTIS, S.T., 2005, *Torridorefugium eskridgensis* (new ichnogenus and ichnospecies): Amphibian aestivation burrows from the Lower Permian Speiser Shale of Kansas: Journal of Paleontology, v. 79, p. 583–593.

HERBST, M., and BENNETT, N.C., 2006, Burrow architecture and burrowing dynamics of the endangered Namaqua dune mole rat (*Bathyergus janetta*) (Rodentia: Bathyergidae): Journal of Zoology, v. 270, p. 420–428.

HICKMAN, C.G., 1990, Adaptiveness of tunnel system features in subterranean mammal burrows, *in* Nevo, E., Reig, O.A., eds., Evolution of Subterranean Mammals at the Organismal and Molecular Levels: New York, Wiley-Liss, p. 185–210.

HILDEBRAND, M., 1974, Analysis of Vertebrate Structure: New York, John Wiley & Sons, 710 p.

HORWATH, J.L., and JOHNSON, D.L., 2006, Mima-type mounds in southwest Missouri: expressions of point-centered and locally thickened biomantles: Geomorphology, v. 77, p. 308–319.

HUNT, R.M., XIANG-XUE, X., and KAUFMAN, J., 1983, Miocene burrows of extinct bear dogs: indication of early denning behavior of large mammalian carnivores: Science, v. 221, p. 354–366.

HUUSE, M., SHOULDERS, S.J., NETOFF, D.I., and CARTWRIGHT, J., 2005, Giant sandstone pipes record basin-scale liquefaction of buried dune sands in the Middle Jurassic of SE Utah: Terra Nova, v. 17, p. 80–85.

IRMIS, R.B., 2005, A review of the vertebrate fauna of the Lower Jurassic Navajo Sandstone in Arizona: Mesa Southwest Museum Bulletin, v. 11, p. 55–71.

JARVIS, J.U.M., and BENNETT, N.C., 1991, Ecology and behavior of the family Bathyergidae, *in* Sherman, P.W., Jarvis, J.U.M., Alexander, R.D., eds., The Biology of the Naked Mole-Rat: Princeton, N.J., Princeton University Press, p. 66–69.

JARVIS, J.U.M., and SALE, J.B., 1971, Burrowing and burrow patterns of east African mole-rats *Tachyoryctes, Heliophobius, Heterocephalus*: Journal of Zoology (London), v. 163, p. 451–479.

JARVIS, J.U.M., O'RAIN, M.J., BENNETT, N.C., and SHERMAN, P.W., 1994, Mammalian eusociality: a family affair: Trends in Ecology and Evolution, v. 9, p. 47–51.

JENKINS, F.A., JR., and PARRINGTON, F.R., 1976, The postcranial skeletons of the Triassic mammals *Eozostrodon*, *Megazostrodon*, and *Erythrotherium*: Royal Society of London, Philosophical Transactions, v. 273, p. 387–431.

JENKINS, F.A., JR., and SCHAFF, C.R., 1988, The Early Cretaceous mammal *Gobiconodon* (Mammalia, Triconodonta) from the Cloverly Formation in Montana: Journal of Vertebrate Paleontology, v. 8, p. 1–24.

JENKINS, F.A., JR., CROMPTON, A.W., and DOWNS, W.R., 1983, Mesozoic mammals from Arizona: new evidence on mammalian evolution: Science, v. 222, p. 1233–1235.

JI, Q., LUO, Z.-X., and JI, S., 1999, A Chinese triconodont mammal and mosaic evolution of the mammalian skeleton: Nature, v. 398, p. 326–330.

JOHNELS, A.G., and SVENSSON, G.S.O., 1954, On the biology of *Protopterus annectens* (Owens): Arkiv for Zoologi, vol. 7, p. 131–164.

KALISZ, P.J., and DAVIS, W.H., 1992, Effect of prairie voles on vegetation and soils in central Kentucky: American Midland Naturalist, v. 127, p. 392–399.

KERMACK, D.M., 1982, A new tritylodontid from the Kayenta Formation of Arizona: Zoological Journal of the Linnean Society, v. 76, p. 1–17.

KERR, J.G., 1988, On the dry-season habitats of *Lepidosiren*: Proclamation of Zoological Society of London, p. 41–44.

KIELAN-JAWOROWSKA, Z., CIFELLI, R.L., and LUO, Z., 2004, Mammals from the Age of Dinosaurs: Origins, Evolution, and Structure: New York, Columbia University Press, 630 p.

KINLAW, A., 1999, A review of burrowing by semi-fossorial vertebrates in arid environments: Journal of Arid Environments, v. 41, p. 127–145.

KINLAW, A.E., CONYERS, L.B., and ZAJAC, W., 2007, Use of ground penetrating radar to image burrows of the gopher tortoise (*Gopherus polyphemus*): Herpetological Review, v. 38, p. 50–56.

KLAPPA, C.F., 1980, Rhizoliths in terrestrial carbonates: classification, recognition, genesis, and significance: Sedimentology v. 26, p. 613–629.

KRAUS, M.J., and HASIOTIS, S.T., 2006, Significance of different modes of rhizoliths preservation to interpreting paleoenvironmental and paleohydrologic settings: Examples from Paleogene paleosols, Bighorn Basin, Wyoming, U.S.A.: Journal of Sedimentary Research, v. 76, p. 633–646.

KOCUREK, G., 2003, Limits on extreme eolian systems: Sahara of Mauritania and Jurassic Navajo Sandstone examples, *in* Chan, M.A., and Archer, A.W., eds., Extreme Depositional Environments: Mega End Members in Geologic Time: Geological Society of America Special Paper 370, p. 43–52.

KÜHNE, W.G., 1956, The Liassic Therapsid *Oligokyphus*: London, Trustees of the British Museum, 149 p.

LANCASTER, N., 1984, Characteristics and occurrence of wind erosion features in the Namib Desert: Earth Surface Processes and Landforms, v. 9, p. 469–478.

LAUNDRE, J.W., 1993, Effects of small mammal burrows on water infiltration in a cool desert environment: Oecologia, v. 94, v. 43–48.

LEE, A.K., and MERCER, E.H., 1967, Cocoon surrounding desert-dwelling frogs: Science, v. 157, p. 87–88.

LIPS, K.R., 1991, Vertebrate burrows associated with tortoise (*Gopherus polyphemus*) burrows in four habitats in south-central Florida: Journal of Herpetology, v. 25, p. 477–481.

LOCKLEY, M.G., 2005, Enigmatic dune walkers from the abyss: some thoughts on water and track preservation in ancient and modern deserts: Canyon Legacy, v. 54, p. 43–51.

LOCKLEY, M., and HUNT, A.P., 1995, Dinosaur Tracks and Other Fossil Footprints of the Western United States: New York, Columbia University Press, 338 p.

LOCKLEY, M., YANG, S.Y., MATSUKAWA, M., FLEMING, F., and LIM, S.K., 1992, The track record of Mesozoic birds: evidence and implications: Royal Society of London, Philosophical Transactions, Biological Sciences, v. 226, p. 113–134.

LOCKLEY, M., HUNT, A.P., MEYER, C., RAINFORTH, E.C., and SCHULTZ, R.J., 1998, A survey of fossil footprint sites at Glen Canyon National Recreation Area (western USA): a case study in documentation of trace fossil resources at a national preserve: Ichnos, v. 5, p. 177–211.

LOOPE, D.B., 1988, Rhizoliths in ancient eolianites: Sedimentary Geology, v. 56, p. 301–314.

LOOPE, D.B., 2006a, Burrows dug by large vertebrates into rain-moistened Middle Jurassic dunes: The Journal of Geology, v. 114, p. 753–762.

LOOPE, D.B., 2006b, Dry-season tracks in dinosaur-triggered grainflows: Palaios, v. 21, p. 132–142.

LOOPE, D.B., 2008, Life beneath the surface of active Jurassic dunes: burrows from the Entrada Sandstone of south-central Utah: Palaios, v. 23, p. 411–419.

LOOPE, D.B., and ROWE, C.M., 2003, Long-lived pluvial episodes during deposition of the Navajo Sandstone: The Journal of Geology, v. 111, p. 223–232.

LOOPE, D.B., ROWE, C.M., and JOECKEL, R.M., 2001, Annual monsoon rains recorded by Jurassic dunes: Nature, v. 412, p. 64–66.

LOOPE, D.B., EISENBERG, L., and WAISS, E., 2004a, Navajo sand sea near-equatorial Pangea: tropical westerlies, slumps, and giant stromatolites, *in* Nelson, E.P., and Erslev, E.A.,

eds., Field Trips in the Southern Rocky Mountains, USA: Geological Society of America, Field Guide 5, p. 1–13.

LOOPE, D.B., STEINER, M.B., ROWE, C.M., and LANCASTER, N., 2004b, Tropical westerlies over Pangaean sand seas: Sedimentology, v. 51, p. 315–322.

LOVEGROVE, B.G., 1991, Mima-like mounds *(heuweltjies*) of South Africa: the topographical, ecological and economic impact of burrowing animals, *in* Meadows, P.S., and Meadows, A., eds., The Environmental Impact of Burrowing Animals and Animal Burrows: New York, Oxford University Press, p. 183–197.

LOUW, G.N., and SEELY, M.K., 1982, Ecology of Desert Organisms: New York, Longman, 194 p.

LOWE, D.R., 1975, Water escape structures in coarse-grained sediments: Sedimentology, v. 22, p. 157–204.

LUCAS, S.G., and HUNT, A.P., 1990, The oldest mammal: New Mexico Journal of Science, v. 30, p. 41–49.

LUCAS, S.G.., GOBETZ, K.E., ODIER, G.P., MCCORMICK, T., and EGAN, C., 2006, Tetrapod burrows from the Lower Jurassic Navajo Sandstone, Southeastern Utah: New Mexico Museum of Natural History and Science, Bulletin 37, p. 147–154.

LUO, Z.-X., CROMPTON, A.W., and SUN, A.-L., 2001, A new mammaliaform from the Early Jurassic and evolution of mammalian characteristics: Science, v. 292, p. 1535–1540.

LYNCH, C.D., 1980, Ecology of the Suricate, *Suricata suricatta* and Yellow Mongoose, *Cynictis pencillata* with Special Reference to Their Reproduction: Bloemfontein, National Museum Memoirs 14, 145 p.

MACAVOY, E.S., MCGIBBON, L.M., SAINSBURY, J.P., LAWRENCE, H., WILSON, C.A., DAUGHERTY, C.H., and CHAMBERS, G.K., 2007, Genetic variation in island populations of

tuatara (*Sphenodon* spp) inferred from microsatellite markers: Conservation Genetics, v. 8, p. 305–318.

MAGWOOD, J.P.A., 1992, Ichnotaxonomy: A burrow by any other name…?, *in* Mapes, C.G. and West, R.R. (eds.), Trace Fossils: Short Courses in Paleontology, 5, p. 15–33.

MANKIN, P.C., and GETZ, L.L., 1994, Burrow morphology as related to social organization of *Microtus ochrogaster*: Journal of Mammalogy, v. 75, p. 492–499.

MARKWELL, T.J., 1997, Video camera count of burrow-dwelling fairy prions, sooty shearwaters, and tuatara on Takapourewa (Stephens Island), New Zealand: New Zealand Journal of Zoology, v. 24, p. 231–237.

MARTIN, L.D., and BENNETT, D.K., 1977, The burrows of the Miocene beaver *Palaeocastor*, western Nebraska, U.S.A: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 22, p. 173–193.

MAYES, P.J., 2007, The use of burrows and burrow characteristics of the semi-aquatic *Varanus mertensi* (Reptilia: Varanidae): Mertensiella, v. 16, p. 312–321.

MCALLISTER, J., 1988, Lungfish burrows in the Upper Triassic Chinle and Dolores Formations, Colorado Plateau-Comments on the recognition criteria of fossil lungfish burrows: Journal of Sedimentary Petrology, v. 58, p. 365–367.

MCCLANAHAN, L.L. JR., SHOEMAKER, V.H., AND RUIBAL, R., 1976, Structure and function of the cocoon of a Ceratophryd frog: Copeia, v. 1976, p. 179–185.

MCKENNA, M.C., and BELL, S.K., 1997, Classification of Mammals Above the Species Level: New York, Columbia University Press, 547 p.

MEYER, R.C., 1999, Helical burrows as a paleoclimate response: *Daimonelix* by *Palaeocastor*: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 147, p. 291–298.

MILLER, M.F., HASIOTIS, S.T., BABOCK, L.E., ISBELL, J.L., and COLLINSON, J.W., 2001, Tetrapod and large burrows of uncertain origin in Triassic high paleolatitude floodplain deposits, Antarctica: Palaios, v. 16, p. 218–232.

MULDER, C.P.H., and KEALL, S.N., 2001, Burrowing seabirds and reptiles: impacts on seeds, seedlings, and soils in an island forest in New Zealand: Oecologia, v. 127, p. 350–360.

NETOFF, D., 2002, Seismogenically induced fluidization of Jurassic erg sands, South-Central Utah: Sedimentology, v. 49 p. 65–80.

NETOFF, D., and SHROBA, R.R., 2001, Conical sandstone landforms cored with clastic pipes in Glen Canyon National Recreation Area, southeastern, Utah: Geomorphology, v. 39, p. 99–110.

NEVO, E., 1999, Mosaic Evolution of Subterranean Mammals: Regression, Progression, and Convergence: New York, Oxford University Press, 413 p.

NEWMAN, D.G., 1987, Burrow use and population densities of tuatara (*Sphenedon punctatus*) and how they are influenced by fairy prions (*Pachyptila turtur*) on Stephens Island, New Zealand: Herpetologica, v. 43, p. 336–344.

NORRIS, K.S., 1953, The ecology of the desert iguana *Dipsosaurus dorsalis*: Ecology, v. 34, p. 265–287.

NOWAK, R.M., 1991, Walker's Mammals of the World: Baltimore, Johns Hopkins University Press, 1629 p.

NOY-MEIR, I., 1973, Desert Ecosystems: environment and producers: Annual Review of Ecology and Systematics, v. 4, p. 25–51.

OLSON, E.C., and BOLLES, K., 1975, Permo-Carboniferous fresh water burrows: Fieldiana Geology, v. 33, p. 271–290.

PARRISH, J.T., and FALCON-LANG, H.J., 2007, Coniferous trees associated with interdune deposits in the Jurassic Navajo Sandstone Formation, Utah, USA: Palaeontology, v. 50, p. 829–843.

PENNA, M., and SOLÍS, R., 1996, Influence of burrow acoustics on sound reception by frogs *Eupsophus* (Leptodactylidae): Animal Behaviour, v. 51, p. 255–263.

PENNA, M., and SOLÍS, R., 1999, Extent and variation of sound enhancement inside burrows of the frog *Eusophus emiliopugini* (Leptodactylidae): Behavioral Ecology and Sociobiology, v. 47, p. 94–103.

PINDER, A.W., STOREY, K.B., and ULTSCH, G.R., 1992, Estivation and hibernation. *in* Feder, M.E., and Burggren, W.W., eds., Environmental physiology of amphibians: University of Chicago Press, Chicago, p. 250–274.

POOLEY, A.C., 1969. The burrowing behavior of crocodiles: Lammergeyer, v. 10, p. 60–63.

RAINFORTH, E.C., and LOCKLEY, M.G., 1996, Tracking life in a Lower Jurassic desert: vertebrate tracks and other traces from the Navajo Sandstone: Museum of Northern Arizona, Bulletin 60, p. 285–289.

RAND, A.S., and DUGAN, B., 1983, Structure of complex iguana nests: Copeia, v. 1983, p. 705–711.

REICHMAN, O.J., and SMITH, S.C., 1990, Burrows and burrowing behavior by mammals, *in* Genoways, H.H., ed., Current Mammalogy: New York, Plenum Press, p. 197–244.

REICHMAN, O.J., WHITHAM, T.G., and RUFFNER, G.A., 1982, Adaptive geometry of burrow spacing in two pocket gopher populations: Ecology, v. 63, p. 687–695.

RENO, H.W., GEHLBACH, F.R., and TURNER, R.A., 1972, Skin and aestivational cocoon of the aquatic amphibian, *Siren* intermedia le conte: Copeia, v. 1972, p. 625–631.

RICE, A.L., and JOHNSTONE, A.D.F., 1972, The burrowing behavior of the Gobiid fish *Lesueurigobius friesii* (Collett): Zeitschrift für Tierpsychologie, v. 30, p. 431–438.

RIESE, D.J., HASIOTIS, S.H., and ODIER, G., 2011, Synapsid burrows and associated trace fossils in the lower Jurassic Navajo Sandstone, southeastern, Utah, U.S.A., indicates a diverse community living in a wet desert ecosystem: *in press.*

ROMER, A.S., and OLSON, E.C., 1954, Aestivation in a Permian lungfish: Breviora, v. 30, p. 1–8.

RUIBAL, R., and HILLMAN, S., 1981, Cocoon structure and function in the burrowing Hylid frog, *Pternohyla fodiens*: Journal of Herpetology, v. 15, p. 403–408.

SCHMEISSER, R.L., LOOPE, D.B., and WEDIN, D.A., 2009, Clues to the medieval destabilization of the Nebraska Sand Hills, USA, from ancient pocket gopher burrows: Palaios, v. 24, p. 809–817.

SEELY, M.K., and LOUW, G.N., 1980, First approximation of the effects of rainfall on the ecology and energetics of a Namib Desert dune ecosystem: Journal of Arid Environments, v. 3, p. 25–54.

SEILACHER, A., 1992, Quo vadis, ichnology?, *in* Mapes, C.G. and West, R.R. (eds.), Traces Fossils: Short Courses in Paleontology, 5, p. 224–238.

SEILER, W.M., and CHAN, M.A., 2008, A wet interdune dinosaur trampled surface in the Jurassic Navajo Sandstone, Coyote Buttes, Arizona: rare preservation of multiple track types and tail traces: Palaios, v. 23, p. 700–710.

SIDOR, C.A., MILLER, M.F., and ISBELL, J.L., 2008, Tetrapod burrows from the Triassic of Antarctica: Journal of Paleontology, v. 28, p. 277–284.

SMITH, C.F., 1948, A burrow of the pocket gopher (*Geomys bursarius*) in eastern Kansas: Kansas Academy of Science, Transactions, v. 51, p. 313–315.

SMITH, H.M., 1956, Handbook of amphibians and reptiles of Kansas: University of Kansas, Lawrence, 356 p.

SMITH, R.M.H., 1987, Helical burrow casts of therapsid origin from the Beaufort Group (Permian) of South Africa: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 60, p. 155–170.

SMITH, J.J., HASIOTIS, S.T., KRAUS, M.J., and WOODY, D.T., 2008, *Naktodemasis Bowni*: new ichnogenus and ichnospecies for adhesive meniscate burrows (AMB), and paleoenvironmental implications, Paleogene Willwood Formation, Big Horn Basin, Wyoming: Journal of Paleontology, v. 82, p. 267–278.

SPINKS, A.C., and BENNETT, N.C., JARVIS, J.U.M., 2000, A comparison of the ecology of two populations of the common mole-rat, *Cryptomys hottentotus hottentotus:* the effect of aridity on food, foraging and body mass: Oecologia, v. 125, p. 341–349.

STEBBINS, R.C., and COHEN, N.W., 1995, A Natural History of Amphibians: Princeton University Press, Princeton, 316 p.

SUES, H.-D., 1984, Inferences concerning feeding and locomotion in the Tritylodontidae (Synapsida), *in* Reif, W.-E., and Westphal, F., eds., Third Symposium on Mesozoic Terrestrial Ecosystems Short Papers: Tübingen, Tübingen University Press, p. 231–236.

SUES, H.-D., 1985, First record of the trityolodontid *Oligokyphus* (Synapsida) from the Lower Jurassic of western North America: Journal of Vertebrate Paleontology, v. 5, p. 328–335.

SUES, H.-D., 1986a, *Dinnebitodon amarali*, a new tritylodontid (Synapsida) from the Lower Jurassic of western North America: Journal of Paleontology, v. 60, p. 758–762.

SUES, H.-D., 1986b, The skull and dentition of two tritylodontids synapsids from the Lower Jurassic of western North America: Museum of Comparative Zoology at Harvard College, Bulletin 151, p. 217–268.

SUES, H.-D., CLARK, J.M., and JENKINS, F.A., JR., 1994, A review of the Early Jurassic tetrapods from the Glen Canyon Group of the American Southwest, *in* Fraser, N.C. and Sues, H.-D., eds., In the Shadow of the Dinosaurs: Early Mesozoic Tetrapods: New York, Cambridge University Press, p. 284–294.

ŠUMBERA, R., ŠKĽIBA, J., ELICHOVÁ, CHITAUKALI, W.N., and BURDA, H., 2008, Natural history and burrow system architecture of the silvery mole-rat from *Brachystegia* woodland: Journal of Zoology, v. 274, p. 77–84.

TALANDA, M., DZIĘCIOL, S., SULEJ, T., and NIEDŹWIEDZKI, G., 2011, Vertebrate burrow system from the Upper Triassic of Poland: Palaios, v. 26, p. 99–105.

TANNER, L.H., SMITH, D.L., and LUCAS, S.G., 2006, Trace fossils in eolian facies of the Upper Triassic-Lower Jurassic Dinosaur Canyon Member, Moenave Formation, Northern Arizona: Ichnos, v. 13, p. 21–29.

TAYLOR, H.M., 1971, Root behavior as affected by soil structure and strength, *in* Carson, E.W. (ed.), The Plant Root and its Environment. University of Press Virginia, Charlottesville, p. 271–291.

TRAEHOLT, C., 1995, Notes on the burrows of the water monitor lizard, *Varanus salvator*: Malayan Nature Journal, v. 49, p. 103–112.

VLECK, D., 1981, Burrow structure and foraging costs in the fossorial rodent, *Thomomys bottae*: Oecologia, v. 49, p. 391–396.

VOORHIES, M.R., 1974, Fossil pocket mouse burrows in Nebraska: American Midland Naturalist, v. 91, p. 492–498.

VOORHIES, M.R., 1975a, Vertebrate burrows, *in* Frey, R.W., ed., The Study of Trace Fossils: New York, Spring-Verlag, p. 325–350.

VOORHIES, M.R., 1975b, A new genus and species of fossil kangaroo rat and its burrow: Journal of Mammalogy, v. 56, p. 160–176.

WAKE, M.H., 1993, The skull as a locomotor organ, *in* Hanken, J., and Hall, B.K., eds., The Skull. Volume 3: Functional and Evolutionary Mechanisms: The University of Chicago Press, Chicago, p. 197–240.

WINKLER, D.A., JACOBS, L.L., CONGLETON, J.D., and DOWNS, W.R., 1991, Life in a sand sea: biota from Jurassic interdunes: Geology, v. 19, p. 889–892.

ZUG, G.R., VITT, L.J, and CALDWELL, J.P., 2001, Herpetology: San Diego, Academic Press, 630 p.

APPENDIX
Architectural Morphologies

Location	Mound	Segment	Width (cm)	Minimum Height (cm)	Length (cm)	Angle°	Dip
MOUT0801	A	1A-1	5.25	2.72	68.5	1&2=75	–
MOUT0801	A	1A-2	9.07	5.68	42	2&3=160	14
MOUT0801	A	1A-3	7.69	3.03	34.5	1&3=125	–
MOUT0801	A	1A-4	5.19	4	47	3&4=85	27
MOUT0801	A	1A-5	5.33	3.02	24.5	1&5=85	–
MOUT0801	A	1A-6	11.9	6.44	47	5&6=75	–
MOUT0801	A	1A-7	8.64	5.79	55	–	23
MOUT0801	A	1A-9	4.92	3.07	25	–	–
MOUT0801	A	1B-1	5.23	3.93	45	1&2=90	10
MOUT0801	A	1B-2	7.04	3.43	68	–	–
MOUT0801	A	1B-3	5.4	2.7	28	–	24
MOUT0801	A	1B-4	8.54	4.6	33	–	–
MOUT0801	A	2A-1	12.3	2.81	30	1&2=80	23
MOUT0801	A	2A-2	12.6	3.3	67.5	1&3=125	–
MOUT0801	A	2A-3	13	6.17	23	–	41
MOUT0801	A	3A	8.39	4.19	93	–	–
MOUT0801	A	4A	8.7	5.42	80	1&2=105	–
MOUT0801	A	5A	10.2	4.99	103	–	–
MOUT0801	A	5A-1	6.7	2.77	2.7	90	–
MOUT0801	A	6A	9.63	3.8	119	–	–
MOUT0801	A	7A-1	12.58	6.87	66	–	–
MOUT0801	A	7A-2	7.75	4.42	55	–	–
MOUT0801	A	8A	6.78	2.3	53	–	–
MOUT0801	A	9A-1	7.65	4.31	84	–	–
MOUT0801	A	9A-2	6.12	3.54	78	1&2=50	–
MOUT0801	A	9A-3	8.29	4.43	25	–	–
MOUT0801	A	9A-4	7.18	3.3	10	–	–
MOUT0801	A	9A-5	6.5	3.8	25	–	–
MOUT0801	A	10A-1	5.02	2.78	70	1&2=100	–
MOUT0801	A	10A-2	6.68	2.69	80	2&3=80	–
MOUT0801	A	10A-3	6.92	3.41	48	–	–
MOUT0801	A	11A	7.25	2.74	22	–	–
MOUT0801	A	12A	6.8	2.77	26	–	–
MOUT0801	A	13A	7.52	2.16	25	–	–
MOUT0801	A	14A	10.97	4.07	56	–	–

MOUT0801	B	1A	6.59	3.63	223	–	–
MOUT0801	B	2A	9.22	5.44	80	–	–
MOUT0801	B	4A-1	7.57	3.61	46	1&2=67	–
MOUT0801	B	4A-2	10.93	3.54	31	1&3=70	–
MOUT0801	B	4A-3	7.53	2.74	30	–	–
MOUT0801	B	5A-1	10.03	3.59	20	1&2=158	–
MOUT0801	B	5A-2	4.55	1.16	32	2&3=58	–
MOUT0801	B	5A-3	4.77	1.75	29	–	–
MOUT0801	Z	1A	10.1	2.78	90	–	–
MOUT0801	C	1A	8.71	4.54	115	–	–
MOUT0801	C	2A-1	4.6	3.37	76	–	–
MOUT0801	C	2A-2	7.67	3.82	–	1&2=93	–
MOUT0801	C	3A	12.25	3.59	145	–	–
MOUT0801	D	1A-1	15.3	7.82	10	1&5/6=130	–
MOUT0801	D	1A-2	13.19	4.92	28	1&2=60	21
MOUT0801	D	1A-3	7.5	2.12	25	1&3=75	15
MOUT0801	D	1A-4	9.28	5.32	90	1&4=80	–
MOUT0801	D	1A-5	11.36	3.1	53.5	4&5=150	–
MOUT0801	D	1A-6	5.45	2.26	43	–	–
MOUT0801	D	2A	5.91	4.13	133	–	–
MOUT0801	D	3A	9.25	2.3	125	–	–
MOUT0801	D	4A	9.81	6.34	65	–	–
MOUT0801	D	6A-1	7.29	5.18		–	–
MOUT0801	D	6A-2	11.42	3.97	220	–	–
MOUT0801	E	2A	15.1	4.72	117	–	–
MOUT0801	E	3A-1	7.02	2.92	85	–	–
MOUT0801	E	3A-2	9.28	4.25	78	1&2=90	–
MOUT0801	E	3A-3	6	8.21	70	–	–
MOUT0801	E	3A-5	11.26	1.87	67	–	–
MOUT0801	E	6A	10.98	5.85	86	–	–
MOUT0801	E	8A	11.93	3.65	103	–	–
MOUT0801	E	9A	8.58	4.73	135	–	–
MOUT0801	E	10A	10.12	7.26	113	–	–
MOUT0801	E	11A	8.47	4.3	63	–	–
MOUT0801	E	12A	8.15	4.49	27.5	–	–
MOUT0801	E	13A	8	3.91	60	–	–
MOUT0801	E	14A-1	5.05	2.02	16	1&2=155	–
MOUT0801	E	14A-2	6.43	4.15	54	1&3=125	–
MOUT0801	E	14A-3	6.76	3.92	40	2&3=80	–

MOUT0801	E	16A-2	5.92	2.2	70	–	–
MOUT0801	Z	2A	13.5	2.51	49.5	–	–
MOUT0801	Z	3A	10.82	2.61	63	–	–
MOUT0801	E	17A	15	4.61	213	–	–
MOUT0801	D	8A-1	14	2.3	40	1&2=90	–
MOUT0801	D	8A-2	21	3	75	–	–
MOUT0801	D	8A-3	12.72	5.08	36	2&3=40	–
MOUT0801	D	9A	19	1.82	92	–	–
MOUT0801	E	18A	10.22	2.04	150	–	–
MOUT0801	A	15A	14.15	3.14	71	–	–
MOUT0801	A	16A-1	12.73	2.41	36	1&2=110	–
MOUT0801	A	16A-2	6.32			–	–
MOUT0801	A	16A-3	11.26			–	–
MOUT0801	A	17A-1	9.34	2.36	75	1&2=80	–
MOUT0801	A	17A-3	8.27	5.35	37	3&4=90	–
MOUT0801	A	17A-4	8.41	1.5	76	–	–
MOUT0801	E	18A	19	6.28	65	–	–
MOUT0801	E	19A-1	14.78	4.22	24	–	–
MOUT0801	E	19A-2	19.5	6.52	25	–	–
MOUT0801	E	20A-1	12.54	7.21	51	1&2=100	–
MOUT0801	E	20A-2	10.32	2.29	15	2&3=100	–
MOUT0801	E	20A-3	8.35	2.8	29	1&3=160	–
MOUT0801	E	21A	11.53	3.42	163.5	–	–
MOUT0802	A	1A	10.06	4.96	52	–	–
MOUT0802	A	2A-1	10.77	4.98	40	1&2=130	–
MOUT0802	A	2A-2	11.5	6.44	20	–	–
MOUT0802	A	4A	11.8	3.04	83	–	–
MOUT0802	A	5A	9.05	4.45	73	–	–
MOUT0802	A	7A	14.47	9.56	78	–	–
MOUT0802	A	8A	8.74	5.55	78	–	–
MOUT0802	A	9A	9.34	5.76	107.5	–	15
MOUT0802	A	12A-1	8.94	6.71	70	1&2=120	–
MOUT0802	A	12A-2	7.76	3.88	43	1&3=100	–
MOUT0802	A	12A-3	9.33	2.33	54	–	–
MOUT0802	A	12A-4	8.06	6.34	23.5	–	–
MOUT0802	A	16A	9.63	5.31	53.5	–	–
MOUT0802	A	18A	7.25	5.34	58	–	–
MOUT0802	A	20A	8.9	4.76	60	–	–
MOUT0802	A	21A	8.38	4.93	47.5	–	–

MOUT0802	A	22A	10.83	5	120	–	60
MOUT0802	A	23A-1	7.95	5.75	35	–	–
MOUT0802	A	23A-2	10.26	6.72	42	1&2=100	–
MOUT0802	B	1A	10.05	5.25	60	–	–
MOUT0802	B	2A	13.89	5.63	56	–	–
MOUT0802	B	3A	7.47	5.08	33	–	–
MOUT0802	B	4A	8.05	5.82	26.5	–	–
MOUT0802	B	5A	9.21	6.14	37.5	–	–
MOUT0802	B	6A-1	10.78	5.15	280	–	–
MOUT0802	B	6A-2	15.32	–	43.5	–	–
MOUT0802	B	7A	10.01	5.95	61.5	–	–
MOUT0802	B	8A	9.68	6.12	129	–	–
MOUT0802	B	9A	7.18	3.67	85	–	–
MOUT0802	B	10A	11.33	7.62	107	–	–
MOUT0802	B	11A-1	11.58	7.12	76.5	1&3=85	–
MOUT0802	B	11A-2	7.09	2.72	20	2&3=75	–
MOUT0802	B	11A-3	9.16	6.22	42	–	–
MOUT0802	B	12A	8.28	6.43	98	–	–
MOUT0802	B	13A	10.8	8.75	132	–	–
MOUT0802	B	15A	11.46	10.2	20.5	–	–
MOUT0802	B	16A	7.78	6.89	81	–	–
MOUT0802	B	17A	11.4	5.88	80	–	–
MOUT0802	B	18A	8.87	5.12	59.5	–	–
MOUT0802	B	19A	8.49	5.39	35	–	–
MOUT0802	B	20A	7.32	4.7	41.5	–	–
MOUT0802	B	21A	6.34	3.31	73.5	–	–
MOUT0802	B	22A	9.02	4.57	36.5	–	–
MOuT0802	B	23A	9.47	6.05	40	–	–
MOUT0802	B	24A-1	8	5.34	35.5	–	–
MOUT0802	B	24A-2	6.61	4.9	14	1&2=65	–
MOUT0802	B	25A	4.23	2.73	35	–	–
MOUT0802	B	26A	5.05	3.48	29.5	–	–
MOUT0802	B	27A-1	6.77	5.75	20	–	–
MOUT0802	B	27A-2	6.37	4.95	18.5	1&2=75	–
MOUT0802	B	28A	5.95	4.83	42	–	–
MOUT0802	C	3A	12.63	4.93	46.5	–	–
MOUT0802	C	6A-1	8.28	4.65	55	–	–
MOUT0802	C	6A-2	11.35	6.25	19	1&2=85	–
MOUT0802	C	7A	9.14	5.7	63	–	–

MOUT0802	C	10A	7.85	5.26	56	–	–
MOUT0802	C	11A-1	12.15	5.61	88.5	–	–
MOUT0802	C	11A-2	9.75	4.4	20.5	–	–
MOUT0802	C	12A-1	7.12	4.86	23	1&2=105	–
MOUT0802	C	12A-2	9.39	2.94	43.5	2&3=120	–
MOUT0802	C	12A-3	5.29	4.13	48	1&3=135	–
MOUT0802	D	1A	6.92	4.69	62	–	–
MOUT0802	D	3A	6.87	4.18	56.5	–	–
MOUT0802	D	4A-1	7.33	3.81	56	–	–
MOUT0802	D	4A-2	8.74	4.05	19	1&2=120	–
MOUT0802	D	5A-1	10	5.1	62	–	–
MOUT0802	D	5A-2	6.61	3.57	24	–	–
MOUT0802	D	6A-1	6.97	4.77	63.5	1&2=160	–
MOUT0802	D	6A-2	9.79	5.2	26	2&3=65	–
MOUT0802	D	6A-3	8.94	5.36	74	1&3=135	–
MOUT0802	D	7A	8.99	3.21	79.5	–	–
MOUT0802	D	8A	7.5	4.69	58.5	–	–
MOUT0802	D	9A	6.29	4	43	–	–
MOUT0802	D	11A-1	8.63	5.33	48	–	–
MOUT0802	D	11A-2	7.6	4.58	14	2&3=45	–
MOUT0802	D	11A-3	6.29	4.92	22	–	–
MOUT0802	D	12A	7.02	4.45	61	–	–
MOUT0802	D	15A	7.08	4.72	100	–	–
MOUT0802	D	16A	9.69	3.7	64.5	–	–
MOUT0803	A	1A	10.85	4.65	76	–	–
MOUT0803	A	2A-1	9.06	4.68	56	–	–
MOUT0803	A	2A-2	8.24	10.22	47	–	–
MOUT0803	A	3A	12.29	5.75	65	–	–
MOUT0803	A	4A-1	17	8.62	90	1&2=90	–
MOUT0803	A	4A-2	9.29	5.06	31	–	–
MOUT0803	A	4A-3	10.61	4.31	92	1&3=135	–
MOUT0803	A	4A-4	9.2	4.26	116	–	–
MOUT0803	A	5A	11.7	4.87	86.5	–	–
MOUT0803	A	6A-1	9.45	5.57	123	1&2=85	–
MOUT0803	A	6A-2	6.21	4.24	28	–	–
MOUT0803	A	7A-1	8.03	4.26	71	1&2=140	24
MOUT0803	A	7A-2	7.72	4.58	43	–	–
MOUT0803	A	8A-1	10.4	7.8	110	–	–
MOUT0803	A	8A-2	7.88	5.43	40	–	–

MOUT0803	A	10A-1	12.78	6.78	70	1&2=40	–
MOUT0803	A	10A-3	12.83	7.6	73	1&3=140	–
MOUT0803	A	11A-1	15	6.05	75	1&2=95	–
MOUT0803	A	11A-2	8.77	3.3	19	–	–
MOUT0803	A	11A-3	6.56	2.65	19	1&3=80	–
MOUT0803	A	11B-1	–	6.26	58	–	–
MOUT0803	A	11B-2	9.91	4.41	28	–	33
MOUT0803	A	11B-3	8.3	5.11	53	–	–
MOUT0803	A	11B-4	9.7	6.95	42	–	–
MOUT0803	A	11B-5	9.36	4.05	16	–	6
MOUT0803	A	11B-6	7.35	2.93	25	6&7=75	–
MOUT0803	A	11B-7	10.75	6.92	108	–	–
MOUT0804	B	2A-1	8.67	4.15	100	–	–
MOUT0804	B	2A-2	8.24	4.94	35	–	–
MOUT0804	B	3A-1	8.73	4.9	93	1&2=90	–
MOUT0804	B	4A	8.39	2.55	93	–	–
MOUT0804	B	5A	11.28	4.93	172	–	–
MOUT0804	B	6A	8.87	5.58	145	–	–
MOUT0804	B	6B	9.46	3.39	39	–	–
MOUT0804	B	7A	12.16	3.31	143	–	–
MOUT0804	B	8A	10.63	3.96	139	–	–
MOUT0804	B	9A	6.82	3.9	147	–	–
MOUT0804	A	1A	8.32	5.04	103	–	–
MOUT0804	A	2A	11.35	7.57	239	–	–
MOUT0804	A	3A-1	11.73	6	77	1=70	–
MOUT0804	A	3A-2	8.6	4.07	88	2=80	–
MOUT0804	A	3A-3	14.52	5.87	136	–	–
MOUT0804	A	4A	15.3	5.73	75	–	–
MOUT0803	B	12A	35	18	617	–	25
MOUT0803	B	13A	58	18	–	–	–

Measurements of notches in previously collected specimens

Notch #	Width (cm)	Height–protruding horizontally (cm)
1	6.5	1.5
2	7	1
3	7	0.5
4	6	1
5	6.5	1.5
6	5	0.8
7	7	–

Surficial Morphologies of Type II Burrow

Left top side	Length (cm)	Width (cm)	Width to next scratch mark (cm)	Angle of Declination
1	10	0.4	2	22
2	9	0.5	3	14
3	5.5	0.5	2.7	30
4	4.5	–	2.5	28
5	5.4	0.35	–	22
6	2.5	0.4	1.8	21
7	10	0.8	3	20
8	10	0.4	2.8	21
9	20	0.4	1.5	30
10	4.5	0.5	2	25
11	16	0.45	–	–
Left underside				
1	13.5	0.7	1.3	20
2	8.5	0.6	3	20
3	6.5	2	2.5	–
4	5.5	0.8	–	–
Right underside				
1	11	0.6	3	≤ 10
2	3.5	0.65	2.3	≤ 10
3	3	0.6	–	≤ 10
4	10	0.7	3.5	≤ 10
5	13	1.1	2.6	≤ 10
6	15.5	0.7	–	30
7	15	0.6	3.2	≤ 10
8	18.5	–	–	≤ 10